Assèchement des cours d'eau : effets sur les communautés d'invertébrés et la dynamique de la matière organique particulaire

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par **Roland CORTI**

ASSECHEMENT DES COURS D'EAU : EFFETS SUR LES COMMUNAUTES D'INVERTEBRES ET LA DYNAMIQUE DE LA MATIERE ORGANIQUE PARTICULAIRE

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RÉSUMÉ

Les cours d’eau qui cessent de s’écouler périodiquement représentent une part substantielle de l’ensemble des hydrosystèmes. D’un point de vue écologique, ils constituent des mosaïques dynamiques d’habitats terrestres, aquatiques et en transition. Si les effets des assèchements sur les communautés et les processus des habitats aquatiques sont relativement bien étudiés, ils sont méconnus dans les habitats terrestres et en transition. L’objectif de cette thèse était de préciser les effets des cycles d’assèchement et de remise en eau sur les communautés invertébrés terrestres colonisant les lits asséchés des cours d’eau et sur la dynamique de la matière organique particulaire (MOP). Au travers d’une approche de terrain multi-sites et comparative menée en France et en Nouvelle-Zélande, il s’agissait de 1) définir une méthode d’échantillonnage des communautés d’invertébrés des lits asséchés, 2) comprendre l’influence des assèchements sur l’organisation et la dynamique de ces communautés et de celles des zones ripariennes adjacentes, 3) caractériser les flux d’invertébrés et de MOP lors des phases de remise en eau et 4) comprendre le rôle des transitions terrestre-aquatique sur la dégradation de la MOP.

Les résultats montrent que l’utilisation de pièges Barber est plus précise et plus rapide que celle des quadrats pour échantillonner les communautés d’invertébrés. En revanche, l’effort d’échantillonnage à produire est élevé, traduisant une distribution spatiale des espèces complexe. Les communautés d’invertébrés terrestres des lits asséchés sont des sous-échantillons des communautés ripariennes adjacentes et leur composition varie peu le long d’un lit asséché de plusieurs kilomètres. Ces travaux suggèrent que la diversité dans les lits asséchés est déterminée latéralement par un mécanisme de densité-dépendance et longitudinalement par la diversité des micro-habitats et la capacité de dispersion des espèces. Lors des remises en eau, un tiers des espèces sont capables de résister à l’inondation et pourraient ainsi participer aux successions d’invertébrés dans les zones ripariennes. Les assèchements modifient la composition des communautés ripariennes mais ne provoquent pas une diminution du nombre d’espèces, indiquant une faible interdépendance entre les écosystèmes ripariens et aquatiques. Enfin, les remises en eau entrainent vers l’aval de grandes quantités de MOP. Dans les zones de stockage, son taux de décomposition diminue avec la durée des assèchements. Les cours d’eau qui s’assèchent sont donc des réacteurs biogéochimiques ponctués et longitudinaux et pourraient influencer la disponibilité en nutriments dans les réseaux hydrographiques.

Les perspectives de ce travail identifient les recherches à mener afin d’inclure le fonctionnement écologique des cours d’eau qui s’assèchent dans les modèles conceptuels en écologie, de caractériser les interactions potentielles entre les écosystèmes terrestres et aquatiques, et d’intégrer les lits asséchés dans les pratiques de gestion actuelles.

When the rivers run dry: effects on invertebrate communities and the dynamic of particulate organic matter

ABSTRACT

Rivers that periodically cease to flow comprise a substantial proportion of the world's hydrological network. From an ecological perspective, these rivers are dynamic mosaics of terrestrial, aquatic, and transitional habitats. Whereas the effects of flow cessation on the communities and processes occurring in aquatic habitats have been relatively well studied, they are unknown for terrestrial and transitional habitats. The objective of this project was to determine the effects of drying and rewetting cycles on terrestrial invertebrates colonizing dry riverbeds and on the dynamic of particulate organic matter (POM). Using a comparative and multi-site experimental approach conducted in France and New-Zealand, this work aimed at 1) defining a sampling method for terrestrial invertebrate communities, 2) studying the effects of flow cessation on the organization and dynamic of terrestrial invertebrate communities in dry riverbeds and their adjacent riparian zones, 3) characterizing the fluxes of invertebrates and POM that are entrained downstream during rewetting phases and 4) understanding the role of aquatic-terrestrial transitions in riverbeds on the decomposition dynamic of POM.

The results showed that pitfall-trapping was more precise and rapid than the quadrat method at sample invertebrate communities from dry riverbeds. Nevertheless, the sampling effort required was high, indicating that species distribution is spatially complex. Terrestrial invertebrate communities occurring in the dry riverbeds of the two studied rivers were nested subsets of those from adjacent riparian areas, and their composition varies only slightly along a distance of several kilometers. These results suggest that invertebrate diversity in dry riverbeds is determined laterally through density-dependent mechanisms and longitudinally by the diversity of micro-habitats and species dispersal. During river rewetting, one-third of species was able to resist submersion and could participate to riparian invertebrate successions. River drying altered the composition of riparian communities but did not reduce taxonomic richness, suggesting that riparian and aquatic ecosystems were not interdependent in these systems. Finally, rewetting events entrained large quantities of POM downstream. In storage zones, POM decomposition rate decreased with the duration of dry periods. Drying rivers are thus punctuated longitudinal biogeochemical reactors that could influence nutrient availability in river networks.

The perspectives of this work identify that future research needs to include the ecological functioning of drying rivers into conceptual models in ecology, to characterize interactions between aquatic and terrestrial ecosystems and to integrate dry riverbeds into management practices.

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SOMMAIRE

INTRODUCTION

Les zones de transition entre les écosystèmes terrestres et aquatiques jouent un rôle primordial dans le fonctionnement des écosystèmes, en régulant les flux d'énergie et de matière tels que les organismes ou les nutriments (Kolasa & Jalewski 1995, Wiens 2002). Dans les cours d'eau, ces zones de transition se déplacent en fonction des variations de débit, latéralement au travers des zones ripariennes, verticalement au sein de la nappe phréatique, mais aussi longitudinalement le long du lit du cours d'eau quand ce dernier connait des périodes d'assèchement (Stanley *et al.* 1997, Doering *et al.* 2007).

Il est aujourd'hui largement reconnu que le mouvement des zones de transition terrestre-aquatique dans la dimension latérale des cours d'eau influencent la biodiversité et les taux des processus écologiques en permettant aux organismes terrestres et aquatiques d'utiliser le même espace à différents moment et de profiter de diverses sources de nutriments. En revanche, les effets des cycles d'assèchement et de remise en eau des lits de cours d'eau sont moins connus (Larned *et al.* 2010). L'essentiel des données disponibles à l'heure actuelle repose sur des études dédiées aux communautés aquatiques (*e.g.* Boulton & Lake 1992, Davey & Kelly 2007, Amalfitano *et al.* 2008, Datry 2012). Les connaissances sur les communautés terrestres et les processus écologiques demeurent très fragmentaires (Larned *et al.* 2010, Steward *et al.* 2012). En conséquence, les cours d'eau qui s'assèchent sont rarement intégrés dans les programmes de gestion des milieux naturels. Pourtant, ils représentent une proportion substantielle de l'ensemble des cours d'eau, estimée entre 30 et 50% en France, en Grèce et aux Etats-Unis (Larned *et al.* 2010). Et leur nombre s'accroit en raison des effets du réchauffement climatique et de la pression qu'exercent les activités humaines sur la ressource en eau.

L'objectif de cette thèse est de préciser les effets des cycles d'assèchement et de remise en eau sur les communautés d'invertébrés terrestres, ainsi que sur dynamique de la MOP, un processus écologique fondamental au fonctionnement des cours d'eau. Au travers de cinq expérimentations de terrain, les recherches ont consistés à 1) définir une méthode d'échantillonnage des invertébrés terrestres dans les lits asséchés, 2) décrire l'organisation des communautés des lits asséchés au regard de celles des zones ripariennes, 3) déterminer les effets des assèchements sur communautés ripariennes, 4) caractériser la composition d'un front de remise en eau en invertébrés et en MOP et 5) préciser le rôle des cycles d'assèchement et de remise en eau sur la décomposition de la MOP par les invertébrés.

ORGANISATION DU DOCUMENT

Le premier chapitre de ce document introduit le cadre conceptuel et les objectifs de recherche. Il présente le rôle écologique des zones de transition terrestre-aquatique au travers du concept d'écotone puis identifie les effets potentiels des cycles d'assèchement et de remise en eau sur les communautés d'invertébrés terrestres et la dynamique de la matière organique. En fin de chapitre, les objectifs de recherche sont développés.

Le deuxième chapitre décrit la méthodologie employée au cours de la thèse. Les sites d'études sélectionnés ainsi que les techniques et méthodes employées pour la réalisation des expérimentations de terrain sont présentés.

Les chapitres 3, 4, 5, 6 et 7 correspondent chacun à un objectif de recherche et sont rédigés sous forme d'articles scientifiques en anglais. Le troisième chapitre compare deux méthodes de collecte des invertébrés terrestres afin de déterminer laquelle est la plus efficace pour échantillonner les communautés des lits asséchés. Le quatrième chapitre caractérise les communautés d'invertébrés terrestres des lits asséchés au regard de celles des zones ripariennes et étudie la variation de la composition des communautés le long d'un secteur de cours d'eau asséché. Le cinquième chapitre analyse les effets des assèchements sur les communautés ripariennes, en comparant les variations temporelles de composition des communautés entre un secteur temporaire et un secteur pérenne d'un même cours d'eau. Le sixième chapitre est consacré à la description de la composition d'un front de remise en eau en invertébrés et en MOP et à sa contribution aux successions d'invertébrés aquatiques. Enfin, le septième chapitre analyse le rôle des cycles d'assèchement et de remise en eau sur la décomposition de la MOP et sa colonisation par les invertébrés terrestres et aquatiques.

Le huitième et dernier chapitre est une synthèse des résultats. La première partie résume les grandes lignes des chapitres précédents et discute leurs implications vis-à-vis des connaissances fondamentales en écologie et des pratiques de gestion des cours d'eau. La deuxième partie présente les perspectives de recherche qui s'inscrivent dans la continuité de cette thèse. Elle esquisse des projets de recherche et des expérimentations visant à mieux comprendre l'organisation des communautés terrestres et aquatiques, leurs interactions dans les C.E.T., ainsi que la dynamique de la MOP dans les réseaux hydrographiques.

1

CADRE CONCEPTUEL ET OBJECTIFS

1.1. LES ZONES DE TRANSITIONS TERRESTRE-AQUATIQUE ET LE CONCEPT D'ECOTONE

Les zones de transition entre les écosystèmes terrestres et aquatiques jouent un rôle primordial dans le fonctionnement global des écosystèmes (Kolasa et Jalewski 1995, Wiens 2002). Ces zones englobent différents milieux caractérisés principalement par la présence temporaire d'eau. Elles partagent certaines propriétés physiques des milieux aquatiques et des milieux terrestres. Ce sont par exemple les zones intertidales en bordure des océans et des mers, les zones littorales des lacs, des marais, marécages et des étangs ou encore les zones ripariennes en bordure des cours d'eau. De manière moins évidente, une zone de transition terrestre-aquatique peut aussi être un cours d'eau qui s'assèche périodiquement. En tant qu'interface entre deux systèmes écologiques adjacents, le rôle écologique des zones de transition est intimement lié au concept d'écotone.

Originellement, le concept d'écotone désigne l'interface entre deux systèmes écologiques différents, cette « zone de tension où les principales espèces des communautés adjacentes atteignent leur limites […], spécialement quand le milieu change, comme entre un étang et une prairie» (Clements 1905). La « zone de tension » possède certaines caractéristiques des deux milieux adjacents mais jamais la totalité de l'un ou l'autre. Les systèmes écologiques adjacents et la zone de transition qui les sépare peuvent être considérés au travers de facteurs biotiques, tels que des communautés d'organismes, des populations et des individus, mais aussi abiotiques, comme le climat, la température ou l'humidité du sol (Gosz 1993). L'écotone abrite des espèces des deux communautés adjacentes et d'autres qui lui sont spécifiques. Il est ainsi perçu comme une zone favorable à une forte diversité d'organismes (Kirkman *et al.* 1998, Attrill & Rundle 2002). C'est « l'effet lisière » (Leopold 1933, Smith & Smith 2008).

A cette approche descriptive est aujourd'hui associée une approche plus fonctionnelle, qui prend en considération les interactions entre les systèmes écologiques adjacents (Forman & Moore 1992). Kolasa & Zalewski (1995) résument le rôle d'un écotone à quatre fonctions principales: ce qu'il fait, son effet retour sur les systèmes écologiques adjacents, sa capacité à réguler les échanges et sa capacité à isoler (**Figure 1.1**). Ainsi, un écotone peut agir comme une source de matériaux, par exemple d'organismes ou de matière organique, mais aussi comme un puits (*e.g.* Peterson & Bell 2012). Il influence les systèmes écologiques qu'il borde, en modifiant les facteurs environnementaux tels que le vent, les flux d'eau ou l'intensité lumineuse (**Figure 1.1a**). Par l'intermédiaire des organismes qu'il supporte, un écotone peut également engendrer un « effet retour », en amplifiant ou en réduisant les processus écologiques qui se déroulent dans les systèmes écologiques adjacents (**Figure 1.1b**) (*e.g.* Odum 1990, Wilson & Agnew 1992). L'écotone régule aussi les flux de matières et d'énergie (*e.g.* gènes, protéines, organismes et nutriments) entre les systèmes écologiques adjacents en jouant le rôle de filtre, à l'image d'une membrane cellulaire (**Figure 1.1c**). Ces flux peuvent être régulés par l'intermédiaire de vecteurs tels que l'eau (Johnston 1993, Wiens *et al.* 1985). Enfin, un écotone peut être une barrière isolant des populations ou des communautés, le degré d'isolement dépendant des organismes considérés (**Figure 1.1d**).

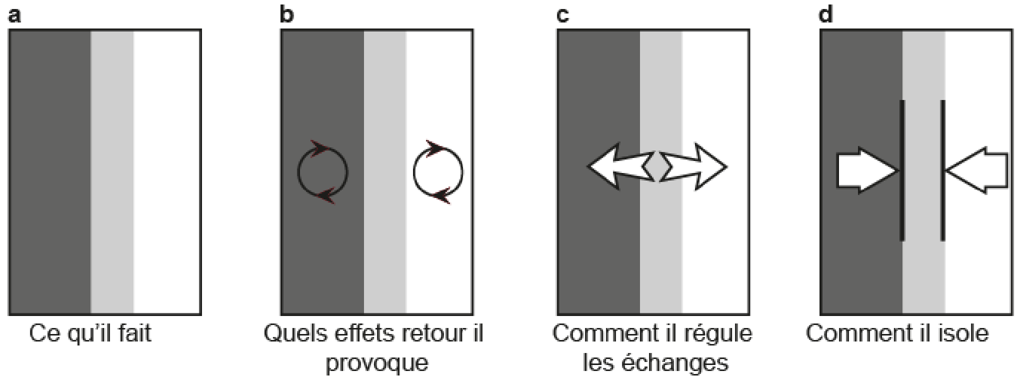


Figure 1.1 Les fonctions de l'écotone sur les deux systèmes écologiques qu'il sépare (modifié d'après Kolasa & Zalewski, 1995).

Les écosystèmes qui sont en transition au sein de l'écotone peuvent être caractérisés à une multitude d'échelles spatiales et temporelles dépendantes du problème considéré (Gosz 1993). Ainsi, des écotones existent à l'échelle du centimètre ou de dizaines de kilomètres. Par exemple, un écotone peut être la zone de transition entre un champ et une forêt mais aussi entre deux biomes comme la Taïga et la Toundra. De plus, un écotone peut contenir d'autres écotones. Les zones de transition sont dynamiques et se modifient dans le temps, horizontalement ou verticalement (Wiens *et al.* 1985, Naiman et Décamps 1997). Par exemple, l'écotone entre les écosystèmes marins et estuariens se déplace au grès des coefficients de marées dans la zone intertidale (Attrill & Rundle 2002), comme la zone de transition entre une rivière et sa zone riparienne se déplace sans cesse en fonction des variations des débits (Gregory *et al.* 1991, Naiman et Décamps 1997).

1.2. ÉCOTONES TERRESTRE-AQUATIQUE DANS LES COURS D'EAU

1.2.1. Les cycles d'expansion et de contraction

Les cours d'eau ne sont pas des écosystèmes statiques (De Vries 1995, Poff *et al.* 1997). À l'échelle d'un bassin versant, la répartition saisonnière des pluies et les échanges entre le cours d'eau et sa nappe phréatique entrainent des variations substantielles des débits et des hauteurs d'eau (Ward *et al.* 1999, Malard *et al.* 2002). À une échelle plus fine l'amplitude journalière des températures peut aussi induire des variations du niveau d'eau en contrôlant localement le phénomène d'évaporation (Claret & Boulton 2003). L'ensemble de ces variations hydrologiques engendre des cycles de contraction et d'expansion des cours d'eau qui par intermittence, inondent ou assèchent les habitats des lits et de la zone riparienne (Naiman & Décamps, Wiens 2002) (**Figure 1.2**).

Les cycles d'expansion et de contraction modifient la nature des habitats dans les dimensions latérale, longitudinale et verticale des cours d'eau (Stanley *et al.* 1997, Malard *et al.* 2006, Doering *et al.* 2007, Datry et Larned 2008). Latéralement, la plaine alluviale est inondée à mesure que le niveau d'eau augmente, et les habitats aquatiques gagnent sur les habitats terrestres (Benke *et al.* 2000, Arscott *et al.* 2009). A l'inverse, les habitats terrestres s'étendent au détriment des habitats aquatiques à mesure que l'effet de la crue s'estompe et que les hauteurs d'eau diminuent (**Figure 1.2**). Verticalement, les variations du niveau piézométrique de la nappe d'accompagnement du cours d'eau peuvent également inonder ou assécher les sédiments sur des profondeurs allant jusqu'à plusieurs mètres (Malard *et al.* 2006). Enfin, longitudinalement, les variations hydrologiques peuvent conduire à la disparition complète de l'eau de surface pour une période allant de quelques heures à plus d'un an. Il se forme alors un front d'assèchement qui s'étend longitudinalement à mesure que le débit diminue, jusqu'à la prochaine remise en eau (Stanley *et al.* 1997, Larned *et al.* 2010).

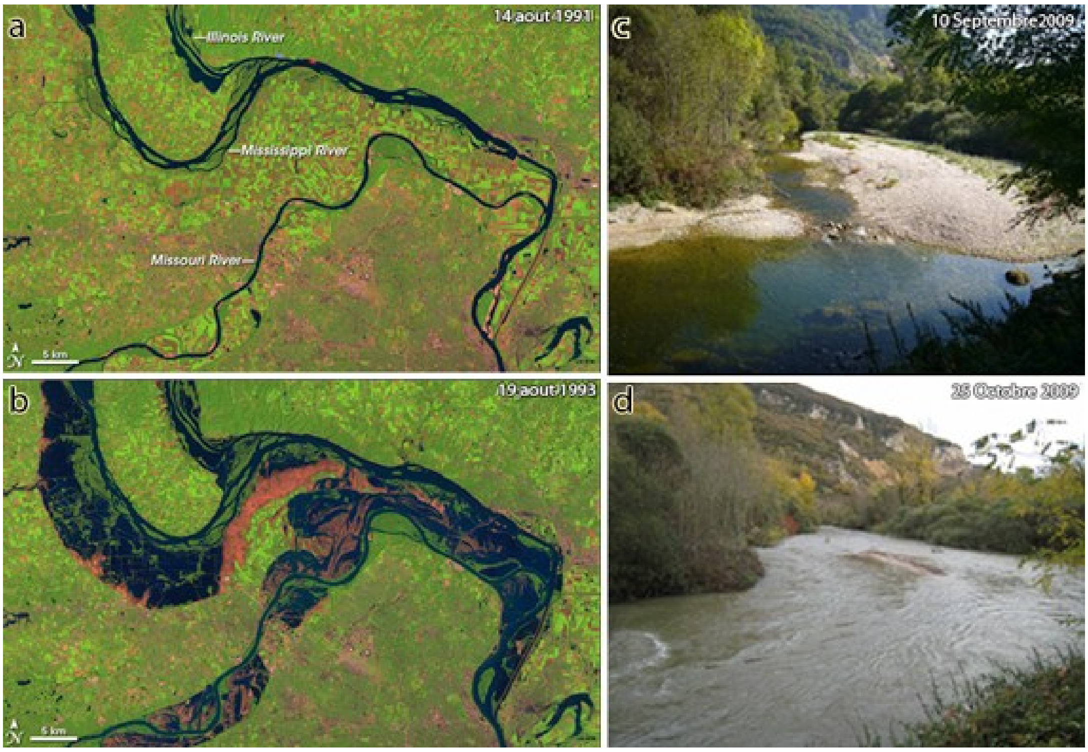


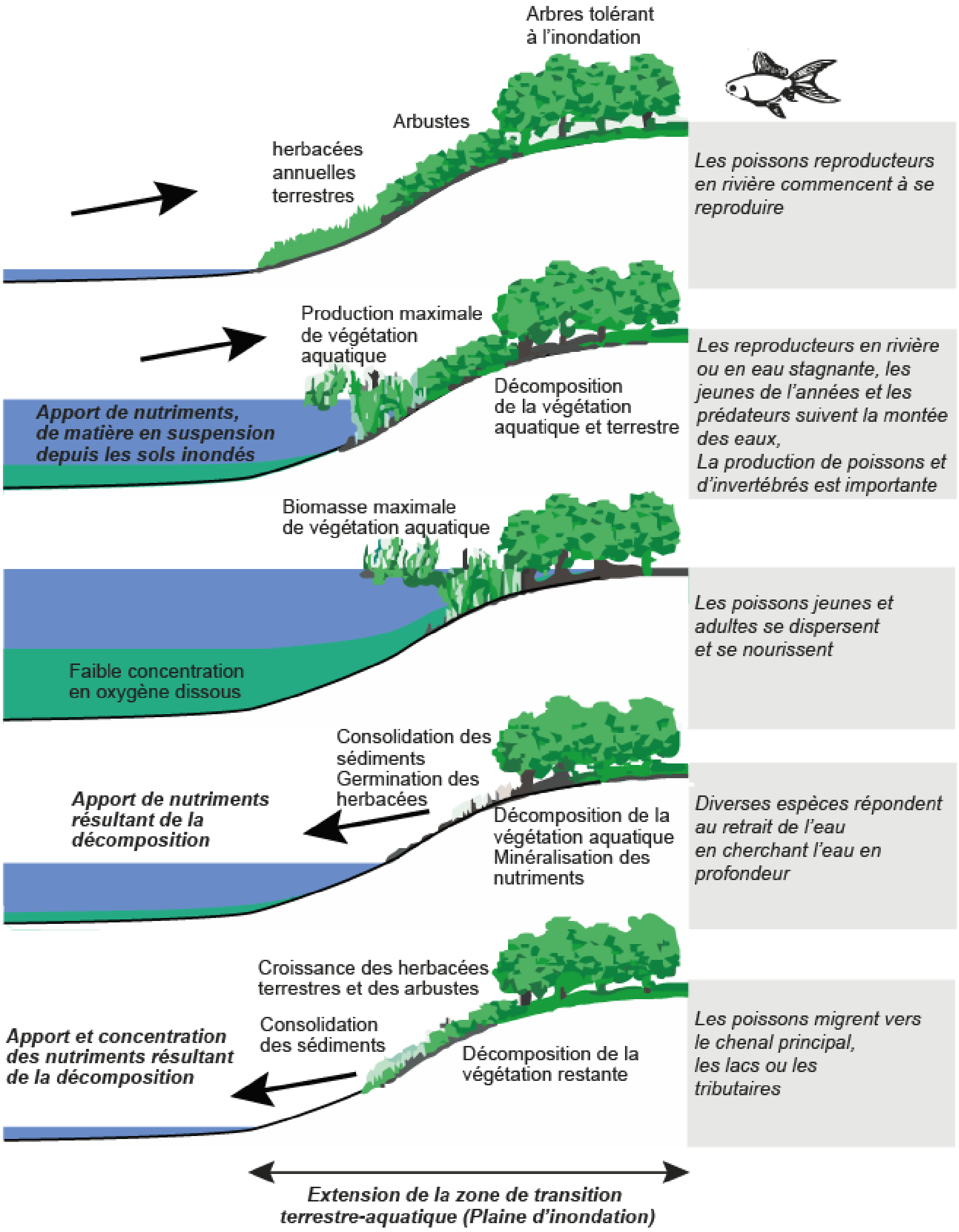
Figure 1.2 Cycles d'expansion et de contraction dans la dimension latérale des cours d'eau. Vues par satellite de la confluence entre le Mississipi, le Misouri et l'Illinois dans dans le Missouri aux Etats-Unis a) en aout 1991 et b) lors de la crue de 1993 (*Source : NASA Earth Observatory*) et photographies de la rivière Albarine en France c) le 10 septembre 2009 et d) le 25 octobre 2009 (*Sources personnelles*)

1.2.2. Rôle écologique des transitions terrestre-aquatique

Les travaux réalisés depuis une quarantaine d'années sur les zones de transition terrestre-aquatique ont donné naissance au « Flood Pulse Concept » (Junk *et al.* 1989), qui est devenu un élément fondamental de l'écologie des cours d'eau. Le « Flood Pulse Concept » se réfère aux processus écologiques liés aux mouvements latéraux de l'eau et des matériaux. Il décrit la dynamique des interactions au sein de la zone de transition terrestre-aquatique. L'idée centrale réside dans le fait que les changements de nature des habitats entre conditions terrestres et aquatiques permettent aux organismes terrestres et aquatiques d'utiliser le même espace à différents moments tout en profitant de diverses sources de nutriments (Tockner *et al.* 2000, Junk 2005), ce qui augmente de manière considérable la biodiversité et la productivité de l'écosystème (Valett 2005, Fellman *et al.* 2013, Roach 2013).

Cinq phases hydrologiques principales peuvent être distinguées pour présenter le « Flood Pulse Concept » (Bayley 1995) (**Figure 1.3**). En période d'étiage, les invertébrés terrestres et les micro-organismes colonisent la plaine alluviale et participent à la dégradation de la matière organique qui s'est développée pendant la crue (Adis & Junk 2002, Ballinger *et al.* 2007). Quand le niveau d'eau augmente, les nutriments contenus dans les sédiments de la plaine alluviale sont mobilisés et initient la production autochtone de végétaux aquatiques. Les micro-organismes et les invertébrés aquatiques participent activement à la décomposition de la matière organique d'origine terrestre accumulée en période d'étiage. Les nutriments ainsi libérés permettent le développement d'une importante biomasse de végétaux aquatiques. Une partie de ces nutriments est remobilisée par les crues et retourne dans le chenal principal où elle participe au développement du phytoplancton. Dans certains cas, la quantité d'oxygène utilisée lors de la décomposition de la matière organique dépasse celle produite par photosynthèse, conduisant à des phénomènes d'anoxie. Le développement de micro-organismes et de la végétation résistante à la submersion fournit une ressource alimentaire ainsi que des milieux de reproduction pour de nombreuses espèces de poissons ou d'invertébrés. À mesure que le niveau d'eau régresse et que la plaine alluviale s'assèche, la végétation aquatique meure et se décompose, ce qui procure une source de nutriments favorable au développement des herbacées et de la végétation arbustive.

L'essentiel des connaissances sur lequel est basé le « Flood Pulse Concept » provient des larges cours d'eau des régions tropicales, où les crues sont prévisibles à l'échelle de la saison et de longue durée (Junk *et al.* 1989). Cependant, les recherches plus récentes montrent que les crues peu prévisibles et qui n'inondent pas nécessairement la plaine alluviale (les « Flow Pulses ») sont fondamentales pour le maintien de la biodiversité dans les cours d'eau tempérés situés en tête ou en fin du réseau hydrographique (Plachter & Reich 1998, Tockner *et al.* 2000). Les phénomènes d'érosion et le remaniement des sédiments lors des crues peuvent engendrer une mosaïque dynamique d'habitats aquatiques et terrestres à différents stades de successions écologiques. L'hétérogénéité des habitats ainsi que les variations spatiales et temporelles des températures de l'eau stimulent la productivité et maintiennent une biodiversité importante dans la plaine d'inondation (Tockner *et al.* 2000).



Les poissons reproducteurs en rivière commencent à se reproduire

Les reproducteurs en rivière ou en eau stagnante, les jeunes de l'années et les prédateurs suivent la montée des eaux,
La production de poissons et d'invertébrés est importante

Les poissons jeunes et adultes se dispersent et se nourissent

Diverses espèces répondent au retrait de l'eau en cherchant l'eau en profondeur

Les poissons migrent vers le chenal principal, les lacs ou les tributaires

Figure 1.3 Représentation schématique du « Flood pulse concept » (Junk *et al.* 1989) montrant un cours d'eau et sa plaine alluviale en fonction de 5 phases d'expansion et de contraction du cours d'eau. La colonne de droite indique les traits d'histoire de vie caractéristiques des poissons. (Modifié d'après Bayley 1995).

De manière concomitante, les zones de transition terrestre-aquatique dans les cours d'eau participent activement aux échanges d'énergie entre les écosystèmes terrestres et aquatiques (Nakano *et al.* 1999, Baxter *et al.* 2005). Par exemple, les invertébrés aquatiques émergents sont une ressource alimentaire fondamentale pour les organismes terrestres prédateurs des zones ripariennes, notamment les araignées (Collier *et al.* 2002, Sanzone *et al.* 2003, Briers *et al.* 2005, Burdon & Harding 2008), les carabes (Hering & Plachter 1997), les lézards (Sabo & Power 2002), et les oiseaux (Nakano & Murakami 2001) (**Figure 1.4**). En parallèle, l'apport de matière organique d'origine terrestre telle que les débris végétaux ou d'invertébrés terrestres dans les écosystèmes aquatiques fournit des ressources alimentaires pour les populations d'invertébrés aquatiques et de poissons (Petersen & Cummins 1974, Kawaguchi *et al.* 2003, Dineen *et al.* 2007). Ainsi, les échanges d'organismes et de matière organique au sein de la zone de transitions terrestre-aquatique ont des conséquences complexes et réciproques sur les chaines alimentaires terrestres et aquatiques qui soutiennent la biodiversité et la production secondaire.

Le « flood pulse concept » et d'autres modèles tels que le « River Continuum Concept » ou le « Hyporheic Corridor Concept » (Vannote *et al.* 1980, Stanford &Ward 1993), ont abouti à une conception plus complexe et réaliste des cours d'eau, intégrant toutes les dimensions des hydrosystèmes (i.e. longitudinale, latérale, verticale et temporelle ; Ward 1989). Pourtant, les connaissances sur lesquelles ces différents concepts sont basés reposent sur des travaux réalisés lors des inondations et assèchements périodiques des zones ripariennes et dans des cours d'eau présentant une connectivité hydrologique amont-aval continue (Datry *et al. in review*). Pendant longtemps, l'assèchement complet du lit des cours d'eau et le développement des zones de transition terrestre-aquatique dans la dimension longitudinale ont été peu considérés par les écologistes. De fait, leur influence sur la biodiversité et les processus biogéochimiques est rarement prise en compte dans les concepts écologiques des cours d'eau (Larned *et al.* 2010, Datry *et al. in review*).

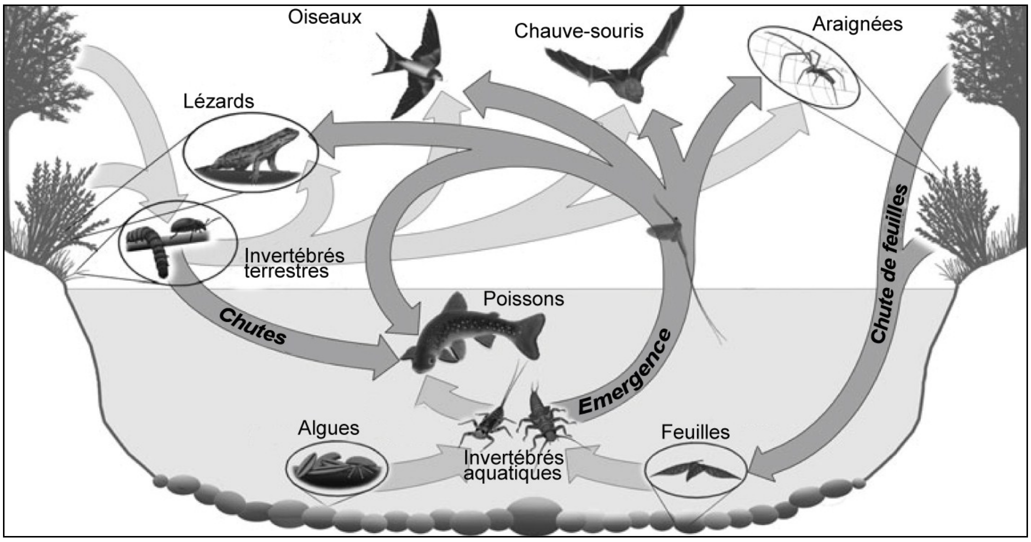


Figure 1.4 Représentation schématique montrant la réciprocité des échanges de proies et de matière organique d'origine végétale au sein des chaînes alimentaires dans le cours d'eau et dans la zone riparienne (d'après Baxter 2005).

1.3. LES COURS D'EAU TEMPORAIRES

1.3.1. L'assèchement des cours d'eau

Le terme « cours d'eau temporaire » (C.E.T.) est utilisé pour définir tous les types de cours d'eau qui s'assèchent périodiquement (Larned *et al.* 2010). L'assèchement survient lorsque les précipitations sont faibles et l'évaporation importante, comme dans les zones arides (Jacobson & Jacobson 2012), mais aussi en raison de l'infiltration des eaux de surface dans la nappe phréatique alluviale (Malard *et al.* 2002, Doering *et al.* 2007) ou lorsque les températures négatives gèlent le mouvement de l'eau au sein d'un bassin versant (McKnight *et al.* 1999, Robinson & Matthaei 2007).

Les cycles d'assèchement et de remise en eau dans les C.E.T. contrôlent le mouvement longitudinal des zones de transition terrestre-aquatique. A mesure que le débit diminue, le cours d'eau se contracte, s'isole de la végétation riparienne, tandis qu'un front d'assèchement s'étend vers l'amont ou l'aval du cours d'eau (Stanley *et al.* 1997, Doering *et al.* 2007). Les radiers sont les premiers à s'assécher et une succession de mouilles isolées se forme (Lake 2003) (**Figure 1.5**). L'abaissement du niveau de la nappe provoque ensuite l'assèchement des mouilles et la disparition complète de l'eau de surface voire l'assèchement de la zone hyporhéique (i.e. les interstices saturés en eau sous les cours d'eau et leurs berges contenant une certaine proportion d'eau de surface - White 1993). L'écoulement de surface est rétabli lorsque des précipitations importantes ou la fonte des neiges provoquent l'avancée sur les sédiments asséchés d'un front de remise en eau. Celui-ci peut prendre la forme d'un mascaret (Jahn 1949, Reid *et al.* 1998, Dunkerley & Brown 1999), d'un ruisseau ou de remontées de nappes (Doering *et al.* 2007). Dans de nombreux C.E.T., la présence de fronts d'assèchement et de remise en eau génère des gradients longitudinaux d'assèchement (Rupp *et al.* 2008, Larned *et al.* 2011), marqués par une augmentation des durées ou des fréquences d'assèchement vers l'aval ou l'amont du cours d'eau.

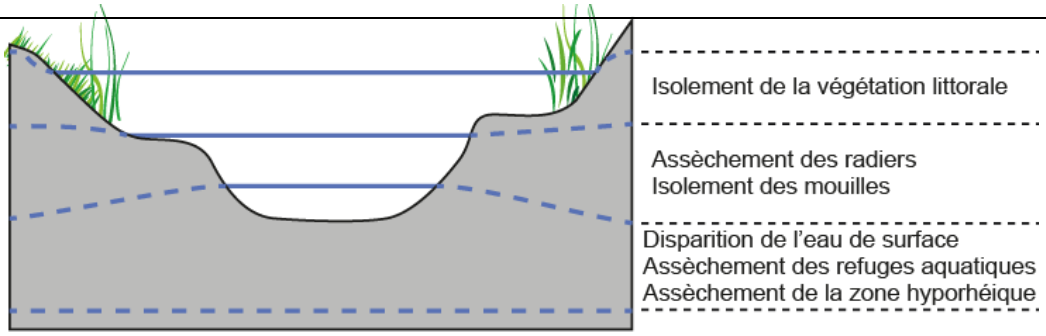


Figure 1.5 Représentation schématique en coupe transversale d'un cours d'eau, montrant les étapes d'assèchement à mesure que le niveau de la nappe d'accompagnement du cours d'eau baisse (modifié d'après Boulton 2003)

1.3.2. Les cours d'eau temporaires dans le monde

Il n'existe à l'heure actuelle aucune estimation globale de l'abondance des C.E.T. dans le monde (Datry et al, in review). Cependant, un survol de la littérature scientifique révèle que les assèchements surviennent sous tous les climats : polaires (McKnight *et al.* 1999, Robinson & Matthaei 2007), tropicaux (Gonçalves *et al.* 2006, Chapman & Kramer 1991), tempérés (Stubbington *et al.* 2009, Datry *et al.* 2011), méditerranéens (Tockner *et al.* 2009), arides et désertiques (Maamri *et al.* 2001, Jacobson *et al.* 2000). Les assèchements peuvent concerner des petits cours d'eau de tête de bassin (Hansen 2001, Dodds *et al.* 2004), tout comme de grands cours d'eau de plusieurs centaines de mètres de largeur (Nadeau & Rains 2007, Doering *et al.* 2007).

Les données concernant la répartition des C.E.T. manquent cruellement dans presque toutes les régions du monde. Quelques travaux, conduits aux Etats-Unis, en Australie, en Afrique du Sud ou en Grèce révèlent que plus de 50% de la longueur totale des cours d'eau de ces pays subissent des assèchements (Nadeau & Rains 2007, Tzorakis & Nikolaidis 2007, Larned *et al.* 2010). À l'échelle de la France, une première modélisation de la répartition des C.E.T. réalisée à partir des données hydrométriques de la Banque Hydro (http://www.hydro.eaufrance.fr/) indique que ceux-ci représenteraient entre 23 et 45% du linéaire des cours d'eau (Snelder *et al.* 2013) (**Figure 1.6**). En définitive, les C.E.T. seraient aussi répandus que les cours d'eau pérennes (Datry *et al.* in review)

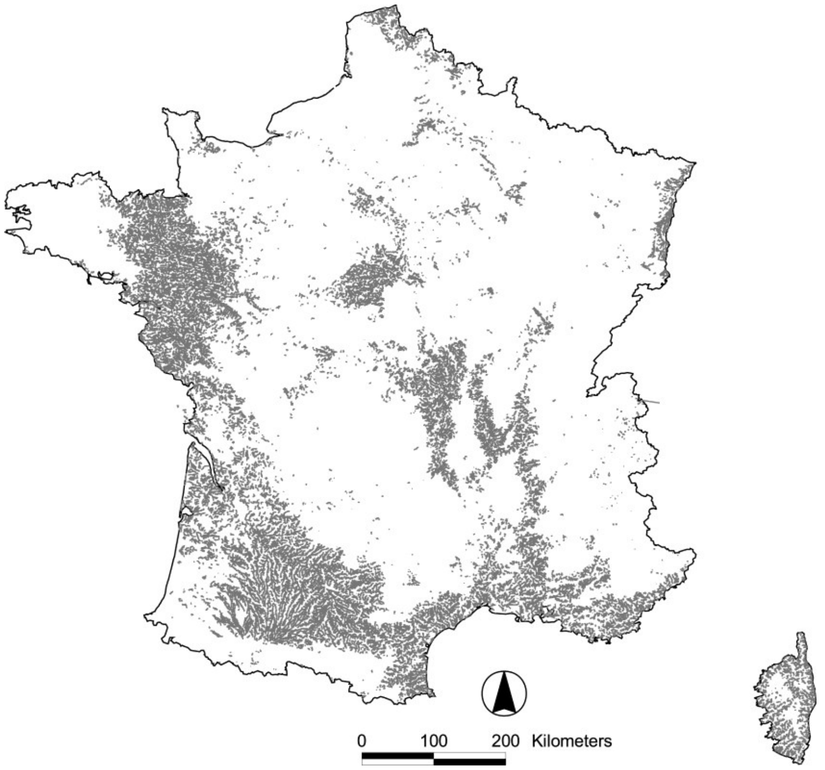


Figure 1.6 Prédiction de la probalité d’assèchement des cours d’eau de France (Snelder *et al.* 2013). L’intensité des traits est fonction de la probablité d’assècheement.

En parallèle à la relative banalité des phénomènes d’assèchement, les simulations sur les effets du réchauffement climatique prédisent une augmentation du nombre de C.E.T. dans de nombreuses régions du monde au cours des prochaines décennies, en raison de la réduction des précipitations et de l’augmentation de l’évapotranspiration (Falke *et al.* 2010, Döll & Müller Schmied 2012). De plus, cette tendance est renforcée par la pression sans cesse croissante qu’exercent les activités humaines sur la ressource en eau (Vörösmarty & Sahagian 2000) (**Figure 1.7.**). Par exemple, l’Arizona a vu s’assécher 35% de ses cours d’eau depuis 200 ans, suite aux prélèvements intensifs d’eau de surface et souterraine (Marshall *et al.* 2010). Désormais, de grands fleuves ou rivières s’assèchent une partie de l’année – comme le Nil, de l’Indus, de l’Amu Darya, du Syr Darya, du Mekong, du Rio Grande, et du Colorado (Postel 2000, Gleick 2003).

Figure 1.7 Photographie aérienne de la Scott River en Californie, USA, un affluent de la Klamath River (source : www.klamathriver.org)

1.3.3. Usages, gestion et perturbations des cours d'eau temporaires

Bien qu'ayant souvent une connotation négative en termes de fonctions et de services écosystémiques, les C.E.T. sont associés à de nombreux usages. Dans un récent article, Steward *et al.* (2012) rapportent que les lits asséchés font souvent partie des cultures traditionnelles au travers d'histoires ancestrales et que de nombreux mots peuvent leur être consacrés, comme par exemple « Uadi » à Magadascar, « Kare-Sawa » au Japon, « Ramblas » en Espagne ou « Warrego » en Australie. Les lits asséchés sont une source de nourriture et d'eau dans de nombreuses régions du monde et plus particulièrement dans les milieux arides (Jacobson *et al.* 1995). Ils sont ainsi utilisés pour le pâturage, l'agriculture, l'extraction de sédiments, et le prélèvement d'eau potable. Dans certaines régions, ils constituent des axes privilégiés de communication (Briggs *et al.* 1993, *in* Steward *et al.* 2012)

En raison d'un manque de connaissances sur le fonctionnement écologique des C.E.T., les gestionnaires des milieux naturels peinent à les intégrer dans les politiques publiques de l'eau. A titre d'exemple, aucune mention n'est faite des C.E.T. et des assèchements dans la Directive Cadre sur l'Eau du 23 octobre 2000 (directive 2000/60) (Logan & Furse 2002). De même aux Etats-Unis, ils sont exclus de la protection par la Clean Water Act de 1972 (Nadeau & Rains 2007). En France, ces cours d'eau, souvent considérés comme atypiques. Ils sont donc rarement intégrés dans les programmes de surveillance de la qualité des eaux, parce que les indicateurs biologiques (*e.g.* IBGN, IPR, IBD) communément utilisés par les gestionnaires des milieux naturels pour évaluer le bon état écologique des masses d'eau ne sont pas fonctionnels dans les C.E.T.

Le manque de reconnaissance sociétale et écologique sur les C.E.T. rend ces derniers particulièrement prompt à subir de multiples perturbations d'origines anthropiques. Le piétinement par le bétail et l'envahissement par les mauvaises herbes ou leur utilisation par véhicules motorisés sont susceptibles d'impacter négativement les C.E.T. (Steward *et al.* 2012). Dans les zones urbaines, ils peuvent être bétonnés et l'exemple le plus caractéristique est certainement celui des célèbres « Ramblas », à Barcelone, en Espagne. De plus, si les activités humaines peuvent être responsables de l'assèchement des cours d'eau (voir section 1.3.2.), certains C.E.T. sont devenus pérennes en raison de la construction de barrages ou de déversoirs ou du fait des rejets d'eaux usées issues des stations d'épuration (Briggs *et al.* 1993, Reich *et al.* 2010).

1.4 BIODIVERSITE ET PROCESSUS ECOLOGIQUES DANS LES COURS D'EAU TEMPORAIRES

1.4.1. Généralités et cadre conceptuel

Les cycles d'assèchement et de remise en eau modifient la nature des habitats au sein du cours d'eau et forment une mosaïque changeante d'habitats. Ceux-ci peuvent être classés comme aquatiques, terrestres ou en transition (Larned *et al.* 2010) (**Figure 1.8**). Les habitats aquatiques peuvent être de petites mouilles persistantes et isolées, ou de longs tronçons pérennes ; les habitats terrestres peuvent être le sommet de rochers émergés, ou de longs secteurs asséchés. La mosaïque d'habitats est multi-scalaire dans le temps et dans l'espace. Dans le temps, la fréquence de transition d'un habitat de l'état aquatique à terrestre, et inversement, varie de moins d'un jour à plus d'un an. Dans l'espace, les habitats aquatiques, en transition et terrestres peuvent être présents au sein d'un même cours d'eau à différents endroits, en fonction de l'avancement ou du retrait du front d'eau (**Figure 1.8**).

Conceptuellement, la mosaïque changeante d'habitats contrôle les successions d'invertébrés terrestres et aquatiques ainsi que les processus écologiques qui leur sont associés (Larned *et al.* 2010). Lors de l'assèchement, les invertébrés aquatiques meurent, développent des formes de résistance ou fuient vers les refuges pérennes (*e.g.* mares et cours d'eau adjacents) (Boulton 1989, Stanley *et al.* 1994, Lake 2003). De même, les flux de matière et d'énergie du cours d'eau vers la zone riparienne cesse (Greenwood & McIntosh 2010). Les habitats asséchés sont alors colonisés par les invertébrés terrestres (Wishart 2000), depuis les zones ripariennes connexes ou d'autres habitats plus éloignés (*e.g.* prairies, forêts). Lors de la remise en eau, les invertébrés terrestres meurent ou fuient vers les refuges tandis que les habitats inondés sont colonisés par les invertébrés aquatiques (Paltridge *et al.* 1997). Les habitats en transition, dans le temps ou dans l'espace, contiennent un mélange d'espèces terrestres et aquatiques et fonctionnent comme des écotones au travers desquels les matériaux, l'énergie et les organismes circulent (Larned *et al.* 2007, Reid *et al.* 2008, Datry *et al.* 2012). Les échanges d'invertébrés aquatiques et terrestres dans les habitats en transition sont susceptibles de soutenir la productivité de l'écosystème (Boulton & Suter 1986, Steward *et al.* 2012). De manière similaire, les cycles d'assèchement et de remise en eau conditionnent le transport et le stockage de la MOP dans les habitats terrestres et aquatiques, et sa décomposition par les invertébrés (Larned *et al.* 2010).

Figure 1.8 Transitions terrestre-aquatique dans la dimension longitudinale des C.E.T. (a, d) Habitats aquatiques, (b, e) habitats en transition (b) mouilles déconnectées, (e) front de remise en eau, (c, f) habitats terrestres. Les photos a, b et c montrent un même site à plusieurs dates ; les photos d, e et f montrent différents sites à la même date. Photos de l'Albarine (01), en France (sources personnelles).

Les connaissances disponibles à ce jour quant aux effets des assèchements sur la biodiversité et les processus écologiques dans les C.E.T. sont relativement récentes (Datry *et al.* 2011). Elles concernent principalement les réponses des communautés aquatiques aux cycles d'assèchement et de remise en eau (*e.g.* Boulton & Lake 1992, Davey & Kelly 2007, Amalfitano *et al.* 2008, Storey & Quinn 2013), et dans une moindre mesure certains processus écologiques essentiels au fonctionnement des cours d'eau, telle que la dynamique de la matière organique particulaire (MOP) (Boulton 1991, Maamri *et al.* 2001). Les réponses des organismes terrestres aux cycles d'assèchement et de remise en eau demeurent très peu étudiées. En raison cette disparité des connaissances vis-à-vis des communautés d'invertébrés et des processus écologiques dans la mosaïque d'habitat, les objectifs du travail de thèse se sont essentiellement focalisés sur les communautés d'invertébrés terrestres et leur influence sur la décomposition de la MOP lors des assèchements et lors de la remise en eau.

1.4.2. Les communautés aquatiques

L'assèchement des cours d'eau influence fortement la composition et la structure des communautés d'invertébrés aquatiques. À mesure que le cours d'eau se contracte, les individus meurent (Lake 2003), s'enfouissent dans la zone hyporhéique (del Rosario & Resh 2000, Stubbington *et al.* 2012), s'envolent grâce à des stades aériens (Williams 2006) ou se concentrent dans des mouilles isolées qui peuvent perdurer jusqu'à la remise en eau (Lake 2003, Robson *et al.* 2011). De nombreuses espèces, résistantes à la dessiccation, peuvent également survivre dans les sédiments asséchés sous formes de kystes, d'œufs ou en dormance, et cela pendant plusieurs jours voire plusieurs mois (Williams 1987, Boulton 1989, Larned *et al.* 2007, Datry *et al.* 2012, Storey & Quinn 2013). Après la remise en eau, la recolonisation des habitats aquatiques est généralement rapide et progressive en fonction des types et des caractéristiques physico-chimiques des refuges disponibles, (Miller & Golladay 1996, Paltridge *et al.* 1997, Fowler 2004, Clarke *et al.* 2010, Datry 212) et implique des mécanismes tels que la dérive, l'oviposition, l'activation des formes de résistance à la dessiccation et la migration depuis la zone hyporhéique (Paltridge *et al.* 1997, Stanley *et al.* 1994, Fritz & Dodds 2004, Sheldon *et al.* 2010, Chester & Robson 2011, Datry 2012).

La comparaison des communautés aquatiques des C.E.T. avec celles des cours d'eau pérennes a souvent donné des résultats contradictoires, révélant une diversité en invertébrés benthiques plus forte (Dieterich & Anderson 2000), similaire (Legier & Talin 1973, Santos & Stevenson 2011) ou plus faible (Meyer & Meyer 2000, Bonada *et al.* 2007, Bogan *et al.* 2013) dans les C.E.T. par rapport aux cours d'eau pérennes. L'utilisation de variables quantitatives pour caractériser les assèchements a permis en partie d'expliquer ces différences : la composition et la structure des communautés aquatiques sont fortement liées à la durée et à la fréquence des périodes d'assèchements (Dodds *et al.* 2004, Larned *et al.* 2007). Ainsi, la richesse taxonomique des invertébrés benthiques et hyporhéiques (Datry *et al.* 2007, Arscott *et al.* 2010, Datry 2012), des poissons (Davey & Kelly 2007, Bond *et al.* 2010) et des plantes ripariennes (Stromberg *et al.* 2009) diminue avec l'augmentation de la durée et de la fréquence des périodes d'assèchement (**Figure 1.9**), et ce, dans de nombreux cours d'eau du monde (Datry *et al. in review*). De plus, les communautés confrontées aux assèchements les plus longs sont des sous-échantillons de celles qui subissent des assèchements moindres, ce qui suggére l'existence d'un faible nombre d'espèces « spécialistes » des C.E.T. (Arscott *et al.* 2010, Datry 2012).

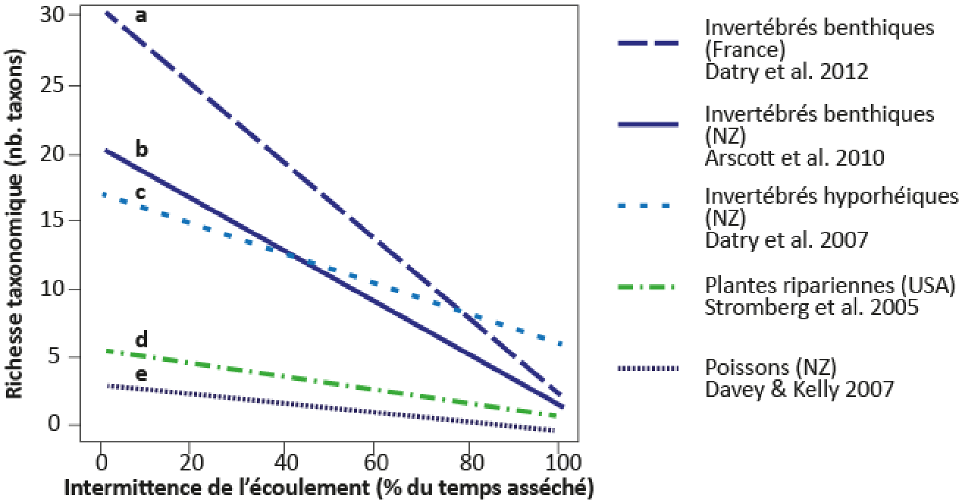


Figure 1.9 Relations entre l'intermittence de l'écoulement et la richesse taxonomique a) et b) des invertébrés benthiques c) des invertébrés hyporhéique, d) des plantes ripariennes et e) des poisons (d'après Datry *et al. in review*)

1.4.3. Les communautés terrestres

Les connaissances sur l'écosystème terrestre des C.E.T. restent à ce jour très parcellaires (Larned *et al.* 2010, Steward *et al.* 2012) et jusqu'à très récemment, les lits asséchés étaient considérés comme biologiquement inactifs (Stanley *et al.* 1997). Pourtant, les travaux réalisés ces dernières années en Afrique du Sud (Wishart 2000), dans le désert de Namibie (André et Jacobson 1997), en Nouvelle-Zélande (Larned *et al.* 2007, Greenwood & McIntosh 2010), en Australie et en Italie (Steward *et al.* 2011) montrent que les lits asséchés sont colonisés par de nombreux invertébrés terrestres dont diversité pourrait dépasser celle des invertébrés aquatiques.

Le manque de connaissances sur les invertébrés terrestres des lits asséchés concerne en premier lieu la caractérisation des communautés d'invertébrés terrestres qu'ils abritent, les variations de leur composition le long de ces lits, les effets des assèchements sur les communautés ripariennes et le devenir des individus lors de la remise en eau. Il est dû en partie à des problèmes d'ordre méthodologique.

L'échantillonnage: un facteur limitant le développement des recherches

L'absence de méthodes d'échantillonnage testées, validées et standardisées pour collecter les invertébrés terrestres dans les lits asséchés contribue certainement au faible développement des recherches les concernants. En effet, l'efficacité des méthodes utilisées dans les forêts, les prairies ou les zones ripariennes (Southwood & Henderson 2000, Zou *et al.* 2012) dépend des groupes taxonomiques et des caractéristiques physiques des habitats considérés (Desender & Segers 1985, Spence & Niemelä 1994, Melbourne 1999, Missa *et al.* 2009). Ainsi, les pièges Barber (Pitfall traps, en anglais) et les quadrats, deux méthodes communément utilisées par les entomologistes, ont donné lieu à de nombreuses études comparatives rapportant des résultats souvent très différents (Desender & Segers 1985, Andersen 1995, Missa *et al.* 2009). A l'heure actuelle, la méthode dite des pièges Barber est la seule à avoir été utilisée dans les lits asséchés. Mais sa précision, son efficacité pour estimer la richesse taxonomique et la composition des communautés ainsi que l'effort d'échantillonnage à produire n'ont jamais été évalués au regard d'une autre méthode.

Des communautés spécifiques des lits asséchés ?

À l'heure actuelle seulement deux études ont décrit les communautés d'invertébrés terrestres des lits asséchés avec suffisamment de précision (Wishart 2000, Steward *et al.* 2011). Elles ont montré que des taxons très divers colonisent ces milieux (*e.g.* araignées, carabes, fourmis, collemboles, hémiptères). Les zones ripariennes sont la source de colonisateurs la plus probable. Dans plusieurs cours d'eau d'Australie et d'Italie, plus de la moitié des invertébrés des lits asséchés étaient communs à ceux des zones ripariennes (Steward *et al.* 2011). Dans les cours d'eau pérennes, les invertébrés ripariens constituent des communautés uniques par rapport à celles des habitats terrestres adjacents (Sabo *et al.* 2005) et fortement dépendantes de la végétation riparienne et de la ressource en eau (Andersen 1985, Hering & Plachter 1997, Paetzold *et al.* 2005). De fait, en raison des températures élevées, de la forte intensité lumineuse (Steward *et al.* 2011) et du faible taux d'humidité des sédiments (Datry *et al.* 2012) qui règnent dans les lits asséchés, ces derniers ne sont probablement pas favorables à tous les invertébrés ripariens. En raison de ces conditions particulières et de la colonisation par des espèces non issues des habitats ripariens, les communautés d'invertébrés des lits asséchés pourraient ne pas être de simples sous-échantillons des communautés ripariennes mais au contraire constituer des communautés spécifiques.

Des communautés structurées dans la dimension longitudinale ?

La plupart des C.E.T., notamment ceux des plaines alluviales, montrent des gradients longitudinaux de durée et de fréquence d'assèchements gouvernés par les échanges hydrique entre la nappe phréatique et le cours d'eau (Rupp *et al.* 2008, Larned *et al.* 2011). Lors des assèchements, ces gradients influencent les caractéristiques physiques et écologiques des habitats des lits asséchés, notamment l'humidité des sédiments et la végétation (Datry *et al.* 2012, Katz *et al.* 2012), deux variables auxquelles les invertébrés terrestres sont grandement sensibles (Antvogel & Bonn 2001, Rykken *et al.* 2007). En conséquence, les communautés d'invertébrés terrestres des lits asséchés pourraient être structurées longitudinalement, en fonction des conditions environnementales et du stade de colonisation.

Des communautés ripariennes influencées par les assèchements ?

Bien que la dynamique des communautés d'invertébrés ripariens ait été largement étudiée en réponse aux inondations (Uetz 1976, Bonn *et al.* 2002, Bates *et al.* 2007, Lambeets *et al.* 2008), les effets des assèchements sur ces communautés restent à ce jour méconnus. En leur sein figurent de nombreux prédateurs ripariens qui dépendent d'invertébrés aquatiques dont ils se nourrissent principalement (Sanzonne *et al.* 2003, Paetzold *et al.* 2005) et de nombreuses espèces sont hygrophiles, c'est-à-dire qu'elles sont inféodées aux milieux humides (Andersen 1988, Lambeets *et al.* 2009). En conséquence, la diversité des invertébrés pourrait être plus faible dans les zones ripariennes des C.E.T. que dans celles des cours d'eau pérennes en raison de la diminution des invertébrés prédateurs et hygrophiles lors des assèchements (McCluney & Sabo 2012). En parallèle, la diminution de la pression trophique exercée par les prédateurs pourrait engendrer des modifications significatives de la composition des communautés ripariennes dans les C.E.T. Ces différences entre secteurs pérennes et secteurs temporaires sont susceptibles d'être plus marquées en période d'assèchement du fait de la dispersion des individus par envol ou par dérive lors des périodes de remise en eau.

1.4.3. Le rôle des phases de transition

Les fronts d'assèchement et de remise en eau sont des phases de transition des conditions terrestres aux conditions aquatiques et inversement. En raison du changement de nature des habitats, ces transitions impliquent de profondes modifications des communautés d'invertébrés et de la dynamique de la MOP (Larned *et al.* 2010). Le front d'assèchement est de loin la phase de transition la plus documentée (Stubbington *et al.* 2009). Les taxons aquatiques les moins résistants à la dessiccation disparaissent progressivement à mesure que la durée d'asséchement augmente (Larned *et al.* 2007, Datry *et al.* 2012). Simultanément, le lit asséché est rapidement colonisé par les invertébrés terrestres (Larned *et al.* 2007, Datry *et al.* 2012) et ces derniers peuvent utiliser les organismes aquatiques en voie de dessiccation comme une ressource alimentaire (Boulton & Suter 1986, Batzer 2004). Le transport et le stockage de la MOP sont également fortement modifiés dans les C.E.T. par rapport aux cours d'eau pérennes. Lors des assèchements, d'importantes quantités de litière de feuilles s'accumulent sur les sédiments asséchés (Dieter *et al.* 2011) d'où elles seront ensuite remobilisées lors des remises en eau (Reid *et al.* 1998, Jacobson *et al.* 2000, Larned *et al.* 2010).

Les remises en eau représentent une transition souvent brutale et rapide des conditions terrestres vers les conditions aquatiques (Larned *et al.* 2010). D'abord, elles emportent les invertébrés terrestres des lits asséchés vers l'aval et impliquer des taux de mortalité importants. Cependant, comme ceux-ci possèdent de nombreuses adaptations leur permettant de fuir vers des refuges (Lytle & White 2007) ou de survivre à la submersion (Boumezzough & Musso 1983, Lambeets *et al.* 2008), les remises en eau constitueraient un mécanisme de dispersion plutôt qu'un évènement simplement destructeur. Les invertébrés aquatiques pourraient aussi être transportés par le front de remise en eau depuis les secteurs pérennes situés en amont et participer ainsi aux successions écologiques dans les habitats aquatiques nouvellement créés. De manière concomitante, la MOP est susceptible d'être stockée au sein de la section temporaire et/ou exportée à l'aval où, avec les invertébrés terrestres submergés, elle contribueraient à soutenir la productivité des écosystèmes aquatiques. À ma connaissance, cet aspect des C.E.T., notamment la composition des fronts de remise en eau en invertébrés et en MOP reste totalement inexplorée.

1.4.4. La décomposition de la matière organique particulaire

Les assèchements influencent de nombreux processus écologiques fondamentaux pour les cours d'eau. Il en est ainsi de l'apport de MOP par les litières de feuilles issues des forêts ripariennes, puis sa dégradation et sa colonisation par les invertébrés. La composition de la MOP, les quantités transportées et stockées par le cours d'eau et les taux de décomposition influencent les chaînes trophiques, les cycles des nutriments et la disponibilité en habitats (Petersen & Cummins 1974, Wallace *et al.* 1997, Webster *et al.* 2001). Les litières de feuilles sont la ressource alimentaire prédominante des invertébrés aquatiques décomposeurs qui utilisent en premier lieu les feuilles pré-conditionnées par les micro-organismes aquatiques (Chergui & Pattee 1991, Abelho 2008, Jabiol & Chauvet 2012). Les invertébrés décomposeurs et les micro-organismes jouent donc un rôle majeur dans la dégradation et la décomposition des litières de feuilles (Benstead *et al.* 2009, Tank *et al.* 2010).

La décomposition de la MOP est fortement ralentie lors des assèchements, du fait de l'élimination des invertébrés aquatiques décomposeurs (Boulton 1991, Maamri *et al.* 2001). Le taux de décomposition semble étroitement lié à la durée et à la fréquence des assèchements en raison de leurs effets négatifs sur les invertébrés aquatiques (Langhans & Tockner 2006, Datry *et al.* 2011). En revanche, les réponses des micro-organismes et leurs effets sur la décomposition de la MOP sont moins clairs. Certaines études montrent une nette diminution de l'activité microbienne lors des assèchements (Boulton 1991, Datry *et al.* 2011). Au contraire, d'autres rapportent que l'activité microbienne est stimulée par l'alternance des assèchements et des remises en eau (Swift *et al.* 1979, Ryder & Horwitz 1995), suggérant que des remises en eau fréquentes pourraient accélérer la décomposition. De plus, lors des assèchements, les micro-organismes continuent de participer à la décomposition de la MOP, lorsque cette dernière est réhydratée par les pluies ou la rosée (Kuehn *et al.* 2004; Langhans & Tockner 2006). La minéralisation photochimique par les rayons du soleil (Austin & Vivanco 2006) et la colonisation des litières de feuilles par les invertébrés décomposeurs terrestres (Wishart 2000, Steward *et al.* 2011) joueraient aussi un rôle important dans la décomposition de la MOP en conditions terrestres.

1.5. OBJECTIFS DE LA THESE

Ce travail vise à apporter des éléments permettant de mieux comprendre le rôle des cycles d'assèchement et de remise en eau sur l'organisation spatiale et la dynamique des communautés d'invertébrés dans les cours d'eau temporaires ainsi que sur la dynamique de la MOP, notamment en considérant l'aspect terrestre de l'écosystème. Plus précisément, il a pour objectif :

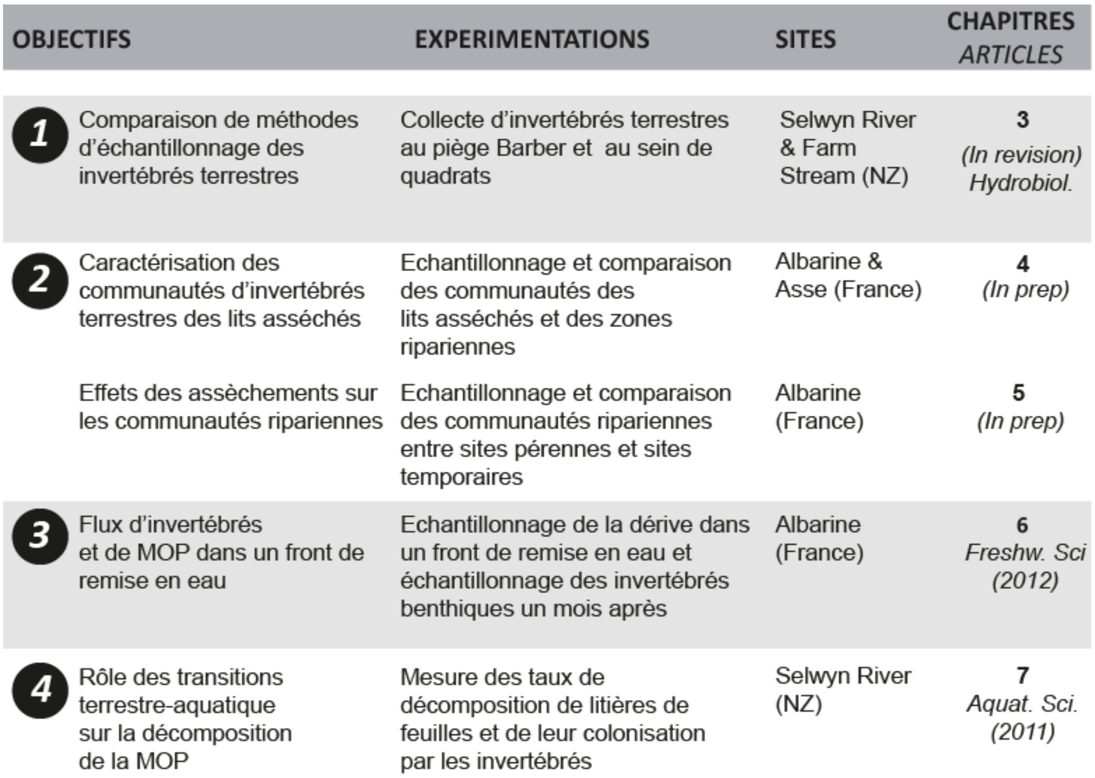
1) de déterminer, parmi deux méthodes de collecte d'invertébrés terrestres, laquelle est la plus efficace pour estimer la richesse taxonomique et de la composition des communautés des lits asséchés

2) de préciser la structure et la composition des communautés des lits asséchés au regard de celles des zones ripariennes adjacentes et de déterminer les effets des assèchements sur l'organisation des communautés d'invertébrés ripariens

3) de caractériser les flux d'invertébrés et de matière organique particulaire dans un front de remise en eau, et la contribution de ce dernier aux successions d'invertébrés aquatiques

4) de comprendre le rôle des transitions terrestre-aquatique dans le lit des cours d'eau sur la dégradation de la MOP et sa colonisation par les invertébrés.

La méthodologie développée dans ce travail repose sur une approche comparative et multi-sites, basée sur 5 expérimentations de terrain (**Figure 1.10**) qui ont consistées à 1) collecter de manière intensive les invertébrés terrestres des lits asséchés de deux C.E.T. à l'aide des pièges Barber et des quadrats 2) échantillonner les communautés d'invertébrés terrestres dans les lits asséchés et les zones ripariennes de deux C.E.T. 3) échantillonner les communautés d'invertébrés ripariens dans les secteurs temporaires et pérennes d'un même cours d'eau, avant et pendant les assèchements 4) échantillonner les invertébrés et la MOP qui dérivent dans un front de remise en eau et échantillonner les communautés benthiques un mois après et 5) mesurer les taux de décomposition de litières de feuilles et leur colonisation par les invertébrés aquatiques et terrestres dans des mouilles subissant un large spectre de durées et de fréquences d'assèchement.



OBJECTIFS	EXPERIMENTATIONS	SITES	CHAPITRES *ARTICLES*
1 Comparaison de méthodes d'échantillonnage des invertébrés terrestres	Collecte d'invertébrés terrestres au piège Barber et au sein de quadrats	Selwyn River & Farm Stream (NZ)	**3** *(In revision) Hydrobiol.*
2 Caractérisation des communautés d'invertébrés terrestres des lits asséchés	Echantillonnage et comparaison des communautés des lits asséchés et des zones ripariennes	Albarine & Asse (France)	**4** *(In prep)*
Effets des assèchements sur les communautés ripariennes	Echantillonnage et comparaison des communautés ripariennes entre sites pérennes et sites temporaires	Albarine (France)	**5** *(In prep)*
3 Flux d'invertébrés et de MOP dans un front de remise en eau	Echantillonnage de la dérive dans un front de remise en eau et échantillonnage des invertébrés benthiques un mois après	Albarine (France)	**6** *Freshw. Sci (2012)*
4 Rôle des transitions terrestre-aquatique sur la décomposition de la MOP	Mesure des taux de décomposition de litières de feuilles et de leur colonisation par les invertébrés	Selwyn River (NZ)	**7** *Aquat. Sci. (2011)*

Figure 1.10 Objectifs de recherche et méthodologie développée dans le cadre de la thèse (expériences réalisées et sites d'études)

2

MATÉRIELS ET MÉTHODES

2.1. LES SITES D'ETUDES

Quatre cours d'eau de France (L'Albarine et l'Asse) et de Nouvelle-Zélande (La Selwyn River et Lower Farm Stream) ont été sélectionnés pour réaliser les expérimentions de terrains (**Figures 2.1 et 2.2**).

2.1.1. L'Albarine

Localisation et caractéristiques générales

L'Albarine s'écoule au cœur du département français de l'Ain, en bordure ouest de la chaîne du Jura (**Figure 2.1a** et **Figure 2.2**). Drainant un bassin versant de 313 km², elle prend sa source à 950 m d'altitude sur le plateau d'Hauteville dans le massif du Bugey puis parcourt une vallée encaissée avant de rejoindre la plaine de la rivière d'Ain dans laquelle elle se jette à 222 m d'altitude. Le linéaire de l'Albarine est marqué par 3 entités morphologiques distinctes (plateau, gorges et plaine) est représente environ 60 km (**Figure 2.1a**). Sa ripisylve est principalement composée de saules (*Salix sp*), d'Aulnes (*Alnus glutinosa*), de peupliers (*Populus sp.*) et de Robinier (*Robinia sp.*).

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Le bassin versant de l'Albarine est exposé à un climat à influences océaniques dégradées, mais des caractéristiques de climat continental peuvent dominer suivant les années à la fin de l'hiver et au début du printemps. Les influences continentales sont sensibles pour le restant de l'année, et font la brièveté des saisons de transition (printemps, automne) (SIABVA, 2008). Les précipitations annuelles moyennes à la confluence avec l'Ain sont de l'ordre de 1150 mm.

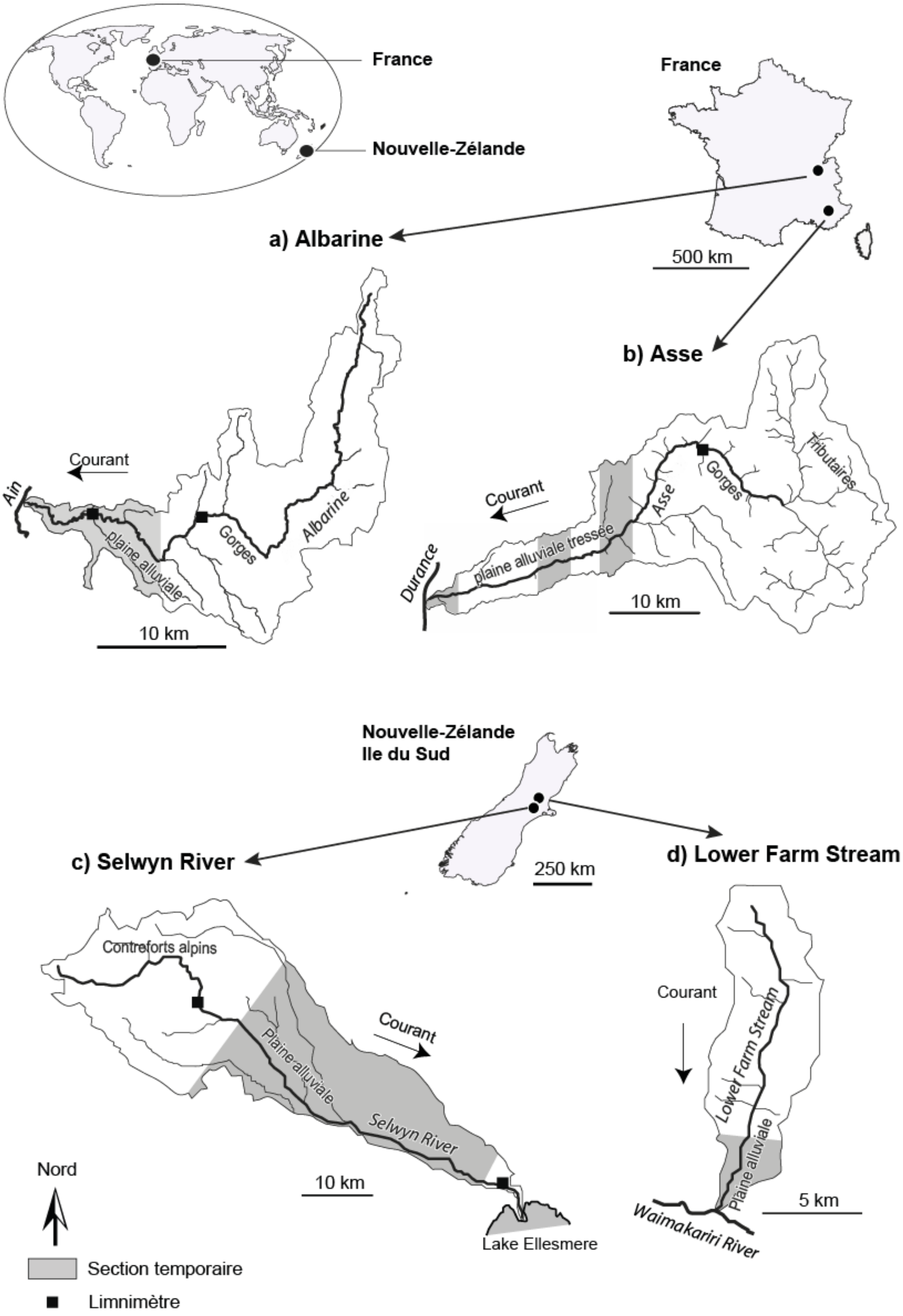


Figure 2.1. Localisation des cours d'eau étudiés en France et en Nouvelle-Zélande

Figure 2.2. Photographies des cours d'eau étudiés en France et en Nouvelle-Zélande

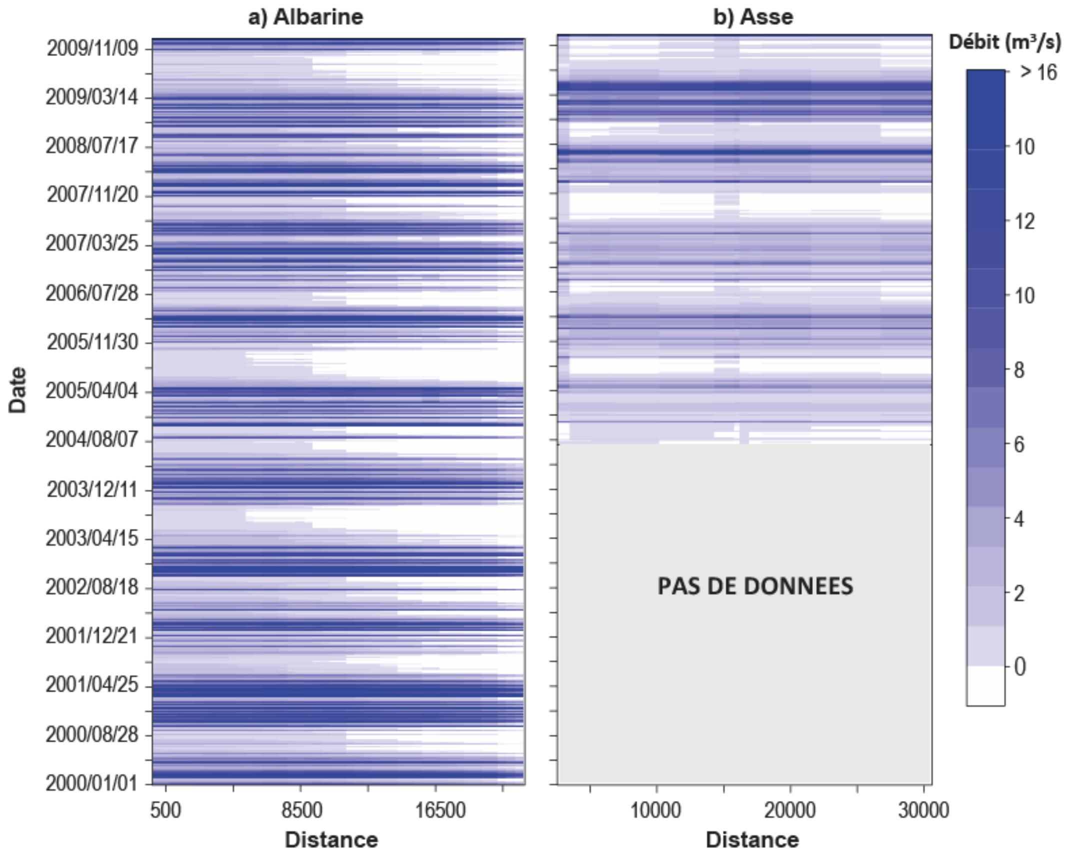
Le régime hydrologique de l'Albarine est pluvio-nival avec une augmentation des débits mensuels moyens autour du mois de mars marquant la fonte des neiges. La rivière est caractérisée par des relations nappe-rivière importantes, complexes et mal connues. Toutefois, trois zones sont identifiées en relation avec trois secteurs géologiques (**Figure 2.1a**). Dans le secteur amont, sur le plateau d'Hauteville, la présence d'un réseau karstique actif engendre des niveaux d'étiage très faibles voire des assecs. En contrebas, la vallée encaissée est influencée par les apports souterrains des résurgences karstiques et la rivière devient pérenne. Plus en aval, dans le secteur de plaine, la rivière se perd dans la nappe phréatique jusqu'à la confluence avec la rivière d'Ain, au travers des sédiments d'origine glacière d'une remarquable perméabilité *(*de l'ordre de 10^{-2} à 10^{-3} m/s*)* (SIABVA, 2008). Du fait de ces pertes massives, le débit de l'Albarine se réduit peu à peu le long du secteur de plaine. Si le débit qui provient du plateau karstique et de la vallée est trop faible (environ 2 m^3/s), alors la rivière commence à s'assécher naturellement d'aval en amont (**Figure 2.2**). Ces assèchements, fréquents tout au long de l'année, mais surtout présents de mai à octobre, génèrent un gradient d'assèchement fortement structuré longitudinalement le long d'une section temporaire de 17 km (SIABVA 2008, Larned *et al.* 2011) (**Figure 2.3a**).

Deux limnimètres enregistrent au pas de temps horaire les débits de la rivière à St Rambert et à St Denis en Bugey depuis 1985. Celui de St Rambert (en amont) montre un module inter annuel de 6,2 m^3/s et un débit annuel bas minimum sur 7 jours de 0,2 m^3/s. Celui situé à St Denis (en aval) montre un module inter annuel de 6,9 m^3/s et un débit annuel bas minimum sur 7 jours de 0 m^3/s.

2.1.2. L'Asse

Localisation et caractéristiques générales

L'Asse s'écoule au cœur du département français des Alpes de Hautes Provence (**Figure 2.1b** et **Figure 2.2**). Drainant un bassin versant de 657 km², c'est un affluent de la Durance en rive gauche. Son linéaire est marqué par 2 entités morphologiques distinctes (gorges et plaine alluviale tressée), qui représentent environ 75 km (**Figure 2.1b)**. Dans la plaine alluviale, la ripisylve est principalement composée de saules (*Salix sp*), d'Aulnes (*Alnus incana*) et de peupliers (*Populus tremula*, *Populus nigra.*).



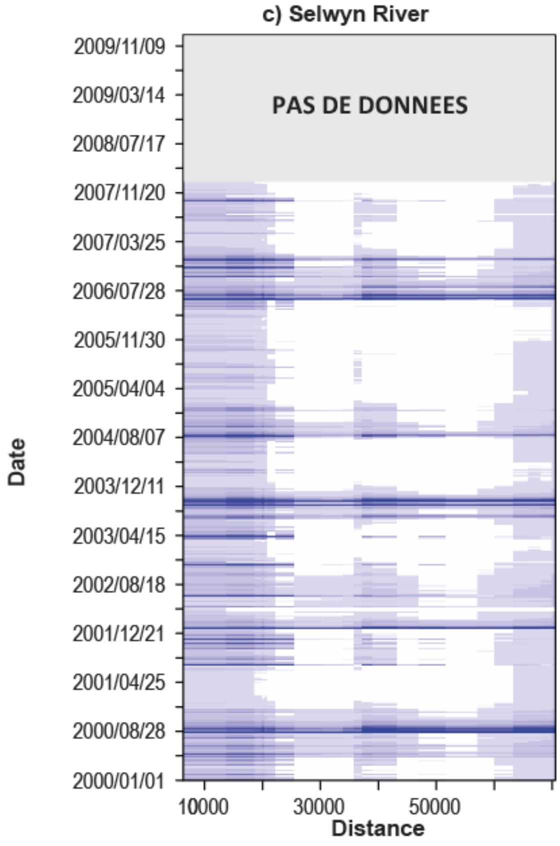


Figure 2.3. Débits journaliers modélisés le long du linéaire a) de l'Albarine b) de l'Asse et c) de la Selwyn River, du 1er janvier 2000 au 31 décembre 2010. Le sens d'écoulement est de la gauche vers la droite, avec la distance en km depuis le limnimètre le plus en amont (cf. Figure 2.1). Les zones blanches correspondent aux secteurs asséchés. Les débits ont été modélisés à l'aide d'ELFMOD, un modèle hydrologique statistique développé en Nouvelle Zélande (Rupp et al. 2008, Larned et al. 2011). Pour estimer les chroniques de débits, le modèle utilise des régressions entre des mesures ponctuelles de débits sur plusieurs stations et les valeurs de débit enregistrées par les limnimètres

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Le bassin versant de l'Asse est exposé à un climat Méditerranéen à influences montagnardes: les étés sont très chauds (températures souvent supérieures à 30°C) et les hivers relativement doux (les températures descendent rarement sous les –5°C). Les précipitations annuelles moyennes à la confluence avec la Durance sont de l'ordre de 933 mm.

Le régime hydrologique de l'Asse est typiquement nival. Le cours d'eau présente régulièrement lors de son parcours dans la plaine alluviale en tresses trois secteurs asséchés lors des étiages estivaux (**Figures 2.1b, 2.2. et 2.3b**). Sa partie terminale (quelques km en amont de la confluence avec la Durance) s'assèche presque chaque année pendant plusieurs semaines (**Figures 2.2 et 2.3b**). Le module inter-annuel naturel de la rivière est estimé à 9,9 m^3/s, avec un débit moyen naturel en juillet de 2,0 m^3/s. En dessous ce cette valeur, les risques d'observer un assèchement à l'aval semblent importants. L'origine de ces assèchements est difficile à déterminer mais repose certainement, comme dans le cas de l'Albarine, sur des pertes d'eau de surface dans la nappe phréatique au travers de sédiments très perméables.

2.1.3. La Selwyn River

Localisation et caractéristiques générales

La Selwyn River s'écoule à l'Est des contreforts alpins de Nouvelle-Zélande dans l'Ile du Sud (**Figure 2.1c** et **Figure 2.2**). Drainant un bassin versant de 975 km², elle se jette dans le lac Ellesmere, en bordure de l'océan pacifique. Son linéaire est marqué par 2 entités morphologiques distinctes : les contreforts alpins et la plaine alluviale de Canterbury, l'ensemble représentant un linéaire d'environ 90 km (**Figure 2.1c)**. Dans la plaine alluviale, la ripisylve est principalement composée de saules (*Salix fragilis*) et de peupliers (*Populus sp.*) (Larned *et al.*, 2008).

Hydrologie, hydrogéologie

Le bassin versant de la Selwyn River est exposé à un climat océanique, avec des températures comprises entre 15 °C et 25 °C en janvier et entre 5 °C et 15 °C en juillet. En été, le vent du Pacifique soufflant du Nord-Est limite la hausse des températures. Les précipitations annuelles moyennes dans la plaine de Canterbury sont de l'ordre de 700 mm (Larned *et al.* 2008).

Le régime hydrologique de la Selwyn River est pluvio-nival. La rivière est marquée par des relations nappe-rivière importantes et complexes (Datry *et al.* 2007, Larned *et al.* 2008). Dans les contreforts alpins, le cours d'eau est pérenne, en raison des fortes précipitations et de la présence de nombreux affluents. Plus en aval, lorsque le cours d'eau atteint la plaine alluviale, la rivière alimente en eau une nappe phréatique peu confinée et composée de sédiments fluvio-glaciaires très perméables (Larned *et al.* 2011). Avant d'atteindre le lac Ellesmere, la nappe phréatique se confine peu à peu, en raison de la présence d'une série verticale de couches géologiques alternant entre des graviers et des argiles (Larned *et al.* 2008). En raison de ce confinement, la nappe phréatique alimente le cours d'eau. Du fait de ces échanges d'eau entre la rivière et la nappe phréatique, la Selwyn River s'assèche dans la partie centrale de la plaine alluviale, comprenant l'aquifère peu confinée, lorsque le débit se réduit peu à peu (**Figure 2.2c**). Le secteur asséché s'étend vers l'amont et vers l'aval, sur une longueur pouvant atteindre 45 km (Larned *et al.* 2011). Dans la partie la plus en aval, les apports d'eau de la nappe phréatique au cours d'eau permettent à ce dernier de s'écouler en permanence. Les assèchements dans la partie centrale de la plaine alluviale sont fréquents tout au long de l'année, mais sont surtout présents au printemps et en été. Ils génèrent un gradient d'assèchement fortement structuré longitudinalement et caractérisé par une section temporaire encadrée par deux sections pérennes en amont et en aval (Larned *et al.* 2011) (**Figure 2.1c**).

Deux limnimètres enregistrent au pas de temps horaire les débits de la rivière, un dans les contreforts alpins et un dans la partie pérenne de la plaine alluviale. Celui situé à l'amont montre un débit moyen de 3.2. m^3/s et un débit annuel bas minimum sur 7 jours de 0,8 m^3/s. Celui situé en aval montre un débit moyen de 3.0 m^3/s et un débit annuel bas minimum sur 7 jours de.5 0 m^3/s.

2.1.4. Lower Farm Stream

Lower Farm Stream est un petit cours d’eau de montagne qui d’écoule à l’Est des contreforts alpins de Nouvelle-Zélande dans l’Ile du Sud (**Figure 2.1c** et **Figure 2.2**). Drainant un bassin versant d’approximativement 6 km², il se jette dans la Waimakariri River. En amont, le cours d’eau s’écoule au travers d’une forêt composée d’espèces natives de Nouvelle-Zélande (*Nothofagus solandri* et *Nothofagus fusca*). A l’aval, la forêt disparait et est remplacée par une végétation basse composée d’herbes de pâturage et de matagouri (*Discaria toumatou*) (Dunn and O’Brien 2007).

Dans sa partie la plus en aval, le cours d’eau s’écoule sur un cône alluvial composé de sédiments très perméable. Les assèchements surviennent en été le long de ce cône alluvial sur 1 à 2 km pendant plusieurs mois lorsque les pertes dans la nappe alluviale dépassent les apports depuis l’amont du bassin versant. Le débit moyen de Lower Farm Stream est de 0.12 m^3/s (Dunn and O’Brien 2007).

2.2. EXPERIMENTATION DE TERRAIN

Cinq expérimentations de terrain ont été réalisées dans le cadre de la thèse. L'expérimentation relative au choix d'une méthode d'échantillonnage des invertébrés terrestres a été réalisée dans les deux cours d'eau de Nouvelle-Zélande (Chapitre 3). L'Albarine et l'Asse ont été utilisées pour caractériser les communautés d'invertébrés terrestres des lits asséchés (Chapitre 4). Les effets de l'assèchement sur les communautés ripariennes ont été étudiés dans l'Albarine, de même que la composition d'un front de remise en eau en invertébrés et en MOP (Chapitre 5 et 6). Enfin, rôle des transitions terrestre-aquatique sur la dégradation de la MOP a été étudié lors d'une expérimentation réalisée dans la Selwyn River (Chapitre 7).

2.2.1. Echantillonnage et identification des invertébrés terrestres

Deux méthodes ont été utilisées pour collecter les invertébrés terrestres : la méthode dite des pièges Barber et la méthode des quadrats. Les pièges Barber sont des pots en plastique de 7 cm de diamètre et de 9 cm de hauteur, enfoncés dans les sédiments jusqu'à ce que la bordure haute du pot atteigne le niveau du sol. Les pièges sont remplis de 15 ml d'éthylène glycol (Cheli and Corley 2010) et sont couverts d'une assiette en plastique pour les protéger de la pluie. Les pièges sont laissés sur place entre 7 et 9 jours. Un quadrat consiste en un cadre en métal de 0,25 m² (50 x 50 cm) posé sur le sol. Pendant 5 minutes, les invertébrés sont collectés au sein du quadrat à l'aide d'un aspirateur à bouche et de pinces, en déplaçant les pierres, les galets et les débris végétaux jusqu'à une profondeur de 10 cm (Andersen 1995).

Les méthodes des pièges Barber et des quadrats ont été comparées pour échantillonner les invertébrés terrestres des lits asséchés en selectionnant 6 sites dans la Selwyn River et dans Lower Farm Stream. Au sein de chaque site, 5 à 36 pièges Barber étaient arrangés en une grille au sein de laquelle 5 à 10 échantillons de quadrats étaient réalisés au moment de la pose et du retrait des pièges Barber (voir chapitre 3).

Afin de caractériser les communautés d'invertébrés terrestres des lits asséchés et d'étudier les effets de l'assèchement sur les communautés ripariennes, une approche comparative et réplicable a été mise en place pour échantillonner les invertébrés terrestres. Huit sites ont été sélectionnés sur l'Albarine et sur l'Asse et ont été échantillonnés à plusieurs dates avant et pendant les assèchements. Sur chaque site, les pièges Barber étaient répartis le long de transects perpendiculaire au lit du cours d'eau. La longueur de chaque site dépendait de la largeur moyenne du chenal actif, défini comme la surface du cours d'eau constituée de sédiments immergés et émergés, bordée de chaque côté par une bande de végétation terrestre et pérenne et différenciée de cette dernière par un changement abrupte de pente. En fonction de la longueur du site, 3 à 5 transects étaient répartis à intervalle régulier le long de chaque site. La longueur de chaque transect était 1,5 × la largeur moyenne du lit mouillée, mesurée au débit moyen annuel. Quatre à sept pièges Barber étaient positionnés le long de chaque transect et espacés de 2 à 3 m, en fonction de la longueur de chaque transect et de la présence ou non d'eau.

Figure 2.4. Collecte des invertébrés terrestres par la méthode des quadrats et des pièges Barber.

Les invertébrés terrestres ainsi collectés ont été identifiés au plus bas niveau taxonomique possible, en fonction des connaissances disponibles. La plupart des coléoptères, des araignées et des fourmis ont été identifiés au genre ou à l'espèce. Les autres taxons (*e.g.* dermaptères, orthoptères, hémiptères, gastropodes) ont été identifiés à la famille, l'ordre ou la classe. L'identification des taxons a été réalisées grâce de l'aide de nombreux collaborateurs (voir section 'remerciements') et en utilisant des collections de référence et de clés de détermination (*e.g.* Gaetan du Chatenet 2005). Les espèces ont été nommées selon la nomenclature du service internet Fauna Europaea (2012). Au total, 42% des individus ont été identifiés à l'espèce, 18% au genre ou à la sous-famille et 40% à la famille, l'ordre ou la classe.

2.2.2. Echantillonnage de la dérive

Les invertébrés et la matière organique en dérive dans un front de remise en eau avançant sur les sédiments asséchés de l'Albarine ont été échantillonnés à l'aide de filets à dérive de 1,5 m de longueur et de maille de 250 µm. Les ¾ seulement de l'ouverture du filet étaient immergés, afin de collecter les invertébrés flottant en surface. Les prélèvements ont été réalisés dans 3 sites pérennes en amont et dans 12 sites en cours de remise en eau et asséchés depuis 4 à 5 mois.

Figure 2.5. Front de remise en eau avançant sur le lit asséché de l'Albarine en novembre 2010.

2.2.3. Mesure du taux de décomposition de la MOP

Les taux de décomposition ont été mesurés dans des mouilles de la Selwyn River par la technique des sacs de feuille. Ceux-ci ont été fabriqués à l'aide d'un grillage de 15 cm de côté et de maille 0,8 cm et rempli avec des feuilles de peuplier (*Populus sp.*).

Figure 2.6. Sacs de litières de feuilles dans les mouilles de la Selwyn River

3

COMPARAISON DE METHODES D’ECHANTILLONNAGE DES INVERTEBRES TERRESTRES DES LITS ASSECHES

Article 1

A comparison of pitfall-trap and quadrat methods for sampling ground-dwelling invertebrates in dry riverbeds

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ABSTRACT

The ground-dwelling invertebrates that inhabit dry beds of temporary rivers are nearly unknown, due in part to the lack of tested, standardized sampling methods. Sampling efficiency and completeness and detection biases associated with pitfall-trap and quadrat samples were compared at six sites in the dry beds of two New Zealand rivers. On average, pitfall-trap samples contained 3.5 times more taxa than quadrat samples, and pitfall traps required less time to collect as many taxa as quadrats. Among all taxa collected, 80% were exclusive to pitfall traps and 4% to quadrat samples. Among-sites differences in invertebrate composition were greater in pitfall-trap samples than in quadrat samples. Rarefaction curves indicated that eight to eleven pitfall traps / 100m² were necessary to collect most of the common taxa in the study sites. Differences in the performance of pitfall traps and quadrats in dry riverbeds may be due to the absence of vegetation, to the large range of taxa considered, and to diel movements of some taxa. The large number of samples required at our study sites to reach a high level of sampling completeness suggests that the diversity of ground-dwelling invertebrates in dry riverbeds has probably been underestimated in previous studies.

Key-words: Temporary rivers; terrestrial invertebrates; sampling efficiency; sampling completeness; detection bias; sampling effort

INTRODUCTION

Temporary rivers are widespread ecosystems whose extent is likely to increase in the future due to global climate and water use changes (Larned *et al.*, 2010; Döll & Müller Schmied, 2012). Temporary rivers have alternating wet and dry phases driven by river flow fluctuations (Stanley *et al.*, 1997). During dry phases, riverbeds are a form of terrestrial habitat and are colonized by ground-dwelling invertebrates (here after referred to as 'terrestrial invertebrates') (Steward *et al.*, 2012). After years of neglect, there is a growing interest in the composition and dynamics of invertebrates in dry riverbeds. This interest is due in part to recent reports of diverse terrestrial invertebrate assemblages in temporary rivers (Wishart, 2000; Steward *et al.*, 2011; Corti & Datry, 2012). However, the spatial and temporal distribution, conservation status, and ecological roles of invertebrates in dry riverbed habitats remain poorly understood.

One of the impediments to studies of terrestrial invertebrates in temporary rivers is the lack of method development and testing. A range of methods have been used in recent investigations, but it is not clear which methods produce the most accurate estimates of assemblage composition, taxonomic richness, and among-site variations of assemblage composition, and how much sampling effort is required. To address these issues and help accelerate research, we compared dry riverbed invertebrate samples collected using two methods widely used by terrestrial ecologists, pitfall trapping and quadrat sampling. A pitfall trap is a cup inserted into sediment into which invertebrates fall and are retained until collection (Southwood & Henderson, 2000). A quadrat sample is a collection of invertebrates made by hand, aspirator or vacuum in a defined area (Andersen, 1995). The pitfall-trap method measures activity densities and quadrat method measure abundance. Both methods are subject to multiple sources of sampling errors and bias due to behavioral and size differences among taxa and to physical characteristics of the sampled habitats (Desender & Segers, 1985; Spence & Niemelä, 1994; Melbourne 1999; Missa *et al.*, 2009). For example, the abundance of highly mobile invertebrates (*e.g.* Carabidae, Araneae) may be overestimated in pitfall traps due to higher catch probabilities (Topping and Sunderland, 1992) and underestimated in quadrat samples due to rapid movement out of quadrats (Uetz & Unzicker, 1976). Pitfall traps may underestimate the abundance of low-mobility taxa or taxa that avoid traps (Greenslade, 1964;

Halsall & Wratten, 1988). Vegetation and rugose sediments can limit the movement of some invertebrates (*e.g.* Carabidae), making pitfall traps more efficient in unvegetated, flat habitat (Melbourne, 1999; Schirmel, *et al.*, 2010). Air and sediment temperature and humidity may affect the behavior of invertebrates and influence their susceptibility to collection by different methods (Honěk, 1988; Desender & Segers, 1985).

Pitfall-trap and quadrat methods have been previously compared in their accuracy in estimating taxonomic richness and assemblage composition of terrestrial invertebrates in forests, grasslands and riverbanks (Uetz & Unzicker, 1976; Andersen, 1995; Tista & Fieldler, 2011). However, dry riverbeds differ from these habitats and the results of the studies comparing pitfall-trap and quadrat data may not be applicable to dry riverbeds. Vegetation is generally absent or very sparse in the active channels of temporary rivers, and soil development is minimal (Kassas & Imam, 1954; Sandercock *et al.*, 2007). Sediment moisture decreases sharply during dry phases (Datry *et al.*, 2012) and air temperatures at sediment surfaces can exceed 70 °C (Steward *et al.*, 2011). Large diel fluctuations in air temperatures and sediment moisture are common in the absence of buffering vegetation (Claret & Boulton, 2003). Physical characteristics of dry riverbeds influence sampling efficiency (defined as the relationship between the sampling effort and the number of taxa collected), detection biases (defined as the inadequacy of a method to detect certain taxa), and sampling completeness (defined as the number of taxa collected as a proportion of the total number of taxa that a method can collect). Detection bias and limited sampling efficiency and completeness can increase uncertainty when characterizing invertebrate assemblages, and when comparing assemblages between locations and between times.

In this study, we collected dry riverbed invertebrates at six different sites in two New Zealand temporary rivers using pitfall traps and quadrats. We used measurements of sampling efficiency, detection bias, and sampling completeness to address three methodological issues: 1) which method is the most efficient for estimating taxonomic richness and assemblage composition at multiple sites; 2) which taxa are best detected by each method; and 3) how does the proportion of total taxonomic richness vary with sampling effort.

METHOD

Study sites

The study was conducted in February 2010 (austral summer) in the Selwyn River and Lower Farm Stream, two alluvial, temporary rivers in southeastern New Zealand. The Selwyn River drains a 975-km^2 catchment to coastal Lake Ellesmere and has a mean annual discharge of 3.0 m^3 s^{-1} (Larned *et al.*, 2008). A 43-km long section of the Selwyn River mainstem between the headwaters and Lake Ellesmere is temporary; this section dries for part of most years. Lower Farm Stream drains a 6-km^2 catchment and flows into the upper Waimakariri River, with a mean instantaneous discharge of 0.12 m^3 s^{-1} (Dunn & O'Brien, 2007). The last kilometer of Lower Farm Stream dries in summer. The duration of dry periods in the temporary sections of both rivers increases with distance downstream.

Six sites in the dry riverbeds of the temporary sections of the Selwyn River (A to C) and Lower Farm Stream (D to F) were sampled for terrestrial invertebrates. Dry riverbeds were defined as active channels with coarse sediment and no perennial vegetation. Sites A and D were located in upstream temporary sections and dried 1 day prior to sampling. Sites B and E were located 0.5 downstream from sites A and D, respectively, and dried ~1 week prior to sampling. Sites C and F were located 2 km downstream from sites A and D, respectively and dried more than one month prior to sampling. At all sites, sediments were dominated by gravels, cobbles, and small boulders. Vegetation at the sampling sites was limited to annual grasses and forbs on the riverbed margins. The study sites at the Selwyn River were bordered by riparian vegetation dominated by small shrubs, annual grasses and forbs with scattered willows (*Salix fragilis*) and cottonwood (*Populus* sp.) trees (Larned *et al.*, 2008). The Lower Farm Stream riparian zone was dominated by annual grasses and matagouri (*Discaria toumatou),* except site F which was bordered by a native forest dominated by mountain beech (*Nothofagus* ssp.) (Dunn & O'Brien, 2007).

Sampling design

At each site, we collected invertebrates in sampling grids composed of 5 to 36 pitfall traps, spaced 3-m apart (Snider & Snider, 1986); 10 to 20 quadrats were sampled between the pifall traps (Figure 1). Spacing between pitfall traps was chosen as a compromise between intensive sampling (i.e., a high number of samples in a minimal area) and minimizing interference among pitfall-traps (Snider & Snider, 1986). At the Selwyn River, 36 pitfall traps (6 x 6 grid) were installed on 3 February 2010 at each site. At the Lower Farm Stream, 20 pitfall traps were installed 3-m apart (4 x 5 grid) on 8 February 2010, except at site D where only 5 pitfall-traps were installed because the riverbed was much narrower. Ten quadrats were sampled at random locations within the Selwyn River sampling grids, and five quadrats were sampled at random locations within the Lower Farm Stream sampling grids. Quadrats were sampled two times at each site, i.e. on the day pitfall traps were installed, and again on the day they were removed (Figure 1). Numbers of pitfall traps and quadrats were based on the maximum number of pitfall traps that could be installed and quadrats that could be sampled at one river in one day. Approximately equal person hours (50-60 min) were allocated to pitfall-trap and quadrat sampling. The area sampled by both methods at each site was approximated as the area covered by the pitfall-trap grids plus half of the distance between 2 pitfall traps on each side.

Collecting methods

Pitfall traps consisted of 7-cm tall, 8-cm diameter plastic containers inserted in sediments until flush with the riverbed surface. Ethylene glycol (15 ml) was added to each container as a preservative, and the containers were covered with a 15-cm diameter plastic plate to keep rain out. All pitfall traps were deployed for 9 days after which the contents were transferred to plastic bags and stored until analysis. The ethylene glycol served as a sample preservative.

Quadrat samples were collected using a square 0.25-m^2 metal frame quickly pressed to the riverbed to limit the escape of individuals (Andersen, 1995). Each sample consisted of a timed 5-min collection of invertebrates using forceps and aspirators. Stones, gravels, and debris were carefully removed by hand to collect invertebrates to a sediment depth of ~10 cm. Invertebrates were preserved in collection containers with 70% ethanol until analysis.

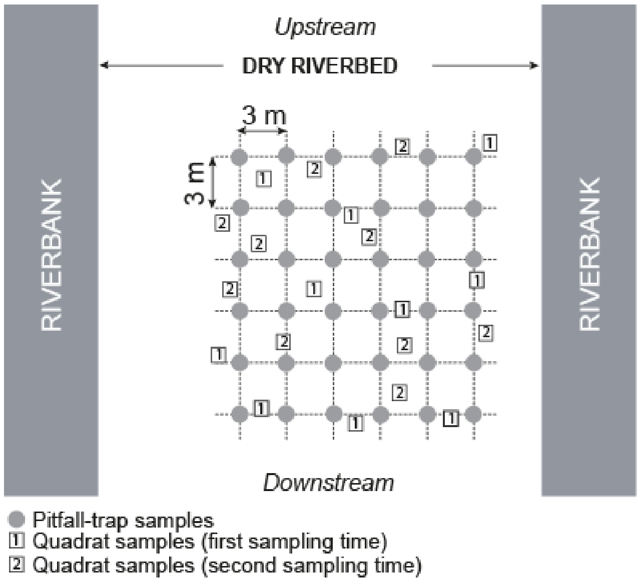

Figure 1. Pitfall-trap and quadrat sample locations at one sampling site. Pitfall-traps were arranged in a grid and positioned 3-m apart. Quadrats were sampled at random points in the grid, on the day pitfall traps were installed, and again on the day they were removed

Laboratory procedures

Invertebrates from pitfall traps were rinsed with tap water above a 63-µm mesh sieve and the retained material was preserved in 70% ethanol. Invertebrates from pitfall traps and quadrat samples were identified to family or higher taxonomic levels, which were then sorted into morphospecies (hereafter referred to as 'taxa') and counted. Morphospecies were defined using morphological characters (*e.g.* number and position of eyes, size, and shape) that are easily observable under a binocular microscope at 10 to 20x magnification (Oliver & Beattie, 1996). Collembola, Acarina, and aerial taxa (*e.g.* Diptera, Apidae, Bombidae, and Lepidoptera) were not included in data analyses as pitfall traps and quadrat searches are not appropriate sampling methods for these taxa (Zou *et al.*, 2012).

Data analysis

Sampling efficiency

Sampling efficiency is defined here as the relationship between the sampling effort and the number of taxa collected. Rarefaction (*sensu* Gotelli & Colwell, 2001) was used to assess differences between pitfall-trap and quadrat samples in the relationships between numbers of samples and taxa occurrences and numbers of taxa. Rarefaction standardizes the sampling effort through random sub-sampling of a dataset and provides the expected number of taxa (S_{exp}) in a given number of samples (Gotelli & Colwell, 2001). Sampled-based rarefaction curves with 95% confidence intervals (CI) were generated using the Mao-Tau function, implemented in the EstimateS 8.2.0 software package (Colwell, 2009) using 100 iterations without replacement. The number of occurrences was used instead of the number of individuals as there were large differences between sampling methods in the number of individuals collected. Differences among methods were considered statistically significant if the confidence intervals around rarefaction curves did not overlap.

Differences in sample collection, rinsing and sorting times for the pitfall-trap and quadrat methods were also compared. Taxa sorting times were estimated by multiplying the average time needed to identify an individual by the average number of individuals in pitfall-trap and quadrat samples. Estimated travel times for pitfall trapping were twice those for quadrat sampling, because two field trips are required to install and retrieve pitfall traps, and one is required for quadrat sampling.

Detection biases

Detection bias associated with pitfall-trap and quadrat sampling were assessed by calculating the proportion of taxa exclusive to each method and shared by both methods. To further represent rare taxa, we calculated the number of singletons (taxa observed once in pitfall-traps and/or quadrat samples) among the exclusive and shared taxa. Rare taxa include those that are present at low numbers in an assemblage, and those that are common in an assemblage, but rarely occur in samples. Differences in the proportion of taxa exclusive to pitfall traps or quadrat samples and the ratio of singletons to exclusive taxa between methods were tested with non-parametric Wilcoxon paired-sample tests (Zar, 2010).

Among-site differences in taxonomic richness and assemblage composition

Sampling efficiency and detection biases can influence the ability of a method to detect among-site differences (Missa *et al.*, 2009). Among-sites differences in taxonomic richness were compared between the two methods within each river using rarefaction curves. We used the Bray-Curtis dissimilarity index to compare invertebrate composition in pitfall-trap and quadrat samples from the three sampling sites at each river. Patterns of dissimilarity were analyzed using non-parametric, non-metric multidimensional scaling (NMDS). Analysis of similarities (ANOSIM) was used to test for differences in assemblage composition among sites. ANOSIM is a non-parametric procedure that evaluates whether the average similarities between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke, 1993). NMDS and the ANOSIM tests were run with invertebrate abundance data, after removal of rare taxa (< 0.1% of individuals). Data were square-root-transformed and double-standardized (Wisconsin method) as necessary, by standardizing taxa by their maxima, and then standardizing samples by sample totals. (Oksanen *et al.*, 2011).

Sampling completeness

Sampling completeness was first addressed graphically by assessing the shapes of rarefaction curves (Gotelli & Colwell, 2001). Next, we calculated the proportions of the total number of taxa reached by the expected number of taxa (S_{exp}) as the number of sample increased (Sackmann *et al.*, 2006). S_{exp} was calculated using Mao-Tau function in EstimateS (Colwell, 2009). The total number of taxa was calculated in two different ways. First, we calculated the maximum expected number of taxa (S_m) at the maximum number of samples collected using the Mao-Tau function. Second, the maximum estimated number of taxa (S_{est}) at the maximum number of samples collected was calculated using the MMMeans estimator in EstimateS (Colwell, 2009). The MMMeans function fits the Michaelis-Menten asymptotic equation to rarefaction curves and calculates the asymptote value. It provided a minimum estimate of the number of taxa that were present at our sampling sites but were not collected (Colwell & Coddington, 1994). Site D was not included in the sampling completeness analysis as there were too few samples to generate an accurate estimate of S_{est}. To facilitate comparisons among methods and sites, the maximum number of samples was set at 20 samples for all sites and for each method, except for quadrat samples at site E and F where the maximum number of samples was set at 10 samples due to the collection of only 10 samples.

Statistical analyses were carried out using R software (R Development Core Team, 2011), except rarefaction curves and MMMeans estimates. NMDS and ANOSIM analyses were carried out using the Vegan R-Package (Oksanen *et al.*, 2011). For all tests, $P < 0.05$ was used to indicate statistical significance.

RESULTS

A total of 51 taxa (45 taxa in pitfall traps and 26 taxa in quadrat samples) and 2913 individuals (2748 from pitfall traps and 165 from quadrat samples) were collected. Pitfall traps contained an average of 4.2 ± 2.0 (± 1 SD) taxa and quadrat samples contained an average of 1.1 ± 1.3 taxa. Four percent of the pitfall traps contained no invertebrates; 43% of the quadrat samples contained no invertebrates. The most abundant taxa in pitfall traps were Carabidae a (Coleoptera), Lycosidae a (Araneae), Opiliones, and Araneae a. The most abundant taxa in quadrat samples were Carabidae a (Coleoptera), Staphylinidae a (Coleoptera), Salticidae (Araneae), and Opiliones (Table 1). These taxa represented more than 50% of the individuals collected with each method (Table 1).

Sampling efficiency

Sample-based rarefaction curves indicated that pitfall traps collected significantly more taxa than quadrat samples (Figure 2a, b). On average, pitfall-trap samples contained 3.5 times more taxa than quadrat samples. The number of taxa from pitfall-trap samples increased with increasing sample numbers more rapidly than the number of taxa from quadrat samples (Figure 2a, b). There was no detectable difference between pitfall-trap and quadrat samples in the number of taxa per occurrence (95% CIs overlapped) (Figure 2c, d). However, the two methods differed in sampling effort; the number of occurrences was 5 to 10-times higher in pitfall-trap samples than in quadrat samples (Figure 2c, d). More than four times more occurrences (and thus samples) would be necessary when quadrat sampling to collect the maximum number of taxa collected when pitfall trapping. The time required to collect and rinse samples and sort individuals from pitfall traps was twice as long as for quadrat samples. On average, 17 min were required to collect a pitfall-trap sample and rinse and sort and sort individuals, while 8 min on average were required to collect a quadrat sample and sort individuals. Therefore, for a similar sampling effort in term of samples or occurrences, pitfall traps required considerably less time to collect as many taxa as quadrat samples. The primary difference in time requirements was for taxa sorting and identification, due to larger numbers of individuals in pitfall traps. However, two field trips are required for each round of pitfall-trap sampling, and a single field trip is required for quadrat sampling.

Table 1 Abbreviation, sum, minimum and maximum, percentage of occurrence (occ, %) and percentage of individuals (%) of taxa shared by pitfall-trap and quadrat samples and exclusive to one or other method

			Pitfall-traps				Quadrats			
Taxa		Abbrev	Sum	Min-Max	Occ	%	Sum	Min-	Occ	%
Shared										
Araneae	Araneae a	Ara a	119	0 - 7	38.0	4.3	3	0 - 1	3.3	1.8
	Araneae e	Ara e	6	0 - 1	3.8	0.2	1	0 - 1	1.1	0.6
	Dolomedes sp.	Dolo	6	0 - 1	3.8	0.2	4	0 - 2	3.3	2.4
	Juvenil	Ara juv	19	0 - 3	8.2	0.7	1	0 - 1	1.1	0.6
	Lycosidae a	Lyco a	240	0 - 12	49.4	8.7	5	0 - 1	5.6	3.0
	Lycosidae c	Lyco c	23	0 - 11	3.8	0.8	1	0 - 1	1.1	0.6
	Lycosidae d	Lyco d	44	0 - 5	14.6	1.6	1	0 - 1	1.1	0.6
	Salticidae	Salti	31	0 - 5	13.9	1.1	14	0 - 4	12.2	8.5
	Supunna picta	Supun	9	0 - 2	5.1	0.3	9	0 - 3	5.6	5.5
Chilopoda		Chilo	3	0 - 1	1.9	0.1	4	0 - 1	4.4	2.4
Coleoptera	Carabidae a	Cara a	1641	0 - 118	59.5	59.7	44	0 - 5	23.3	26.7
	Carabidae c	Cara c	14	0 - 2	8.2	0.5	4	0 - 3	2.2	2.4
	Coccinellidae	Cocci	3	0 - 1	1.9	0.1	2	0 - 1	2.2	1.2
	Coleoptera b	Col b	14	0 - 2	8.2	0.5	2	0 - 2	1.1	1.2
	Staphylinidae a	Staph	28	0 - 3	10.1	1.0	26	0 - 10	8.9	15.8
Hemiptera	Hemiptera	Hemi	4	0 - 1	2.5	0.1	1	0 - 1	1.1	0.6
	Miridae	Mirid	34	0 - 5	11.4	1.2	3	0 - 1	3.3	1.8
Hymenoptera	Myrmicinae	Myrmi	7	0 - 2	3.8	0.3	5	0 - 4	2.2	3.0
Megaloptera		Mega	1	0 - 1	0.6	0.0	2	0 - 1	2.2	1.2
Oniscidea		Onis	12	0 - 4	3.2	0.4	8	0 - 3	4.4	4.8
Opiliones		Opilio	203	0 - 10	51.9	7.4	11	0 - 2	11.1	6.7
Exclusive to pitfall traps samples										
Araneae	Agelenidae	Age	3	0 - 1	1.9	0.1	0	0 - 0	0.0	0.0
	Araneae b	Ara b	2	0 - 1	1.3	0.1	0	0 - 0	0.0	0.0
	Araneae d	Ara d	37	0 - 4	12.7	1.3	0	0 - 0	0.0	0.0
	Lycosidae b	Lyco b	7	0 - 1	4.4	0.3	0	0 - 0	0.0	0.0
	Lycosidae e	Lyco e	27	0 - 6	5.1	1.0	0	0 - 0	0.0	0.0
Blattodea	Blattidae	Blatt	3	0 - 2	1.3	0.1	0	0 - 0	0.0	0.0
Coleoptera	Carabidae b	Cara b	17	0 - 4	7.6	0.6	0	0 - 0	0.0	0.0
	Carabidae d	Cara d	10	0 - 2	5.1	0.4	0	0 - 0	0.0	0.0
	Carabidae e	Cara e	5	0 - 1	3.2	0.2	0	0 - 0	0.0	0.0
	Carabidae f	Cara f	42	0 - 6	13.3	1.5	0	0 - 0	0.0	0.0
	Coleoptera a	Col a	1	0 - 1	0.6	0.0	0	0 - 0	0.0	0.0
	Coleoptera c	Col c	22	0 - 3	8.2	0.8	0	0 - 0	0.0	0.0
	Coleoptera d	Col d	3	0 - 1	1.9	0.1	0	0 - 0	0.0	0.0
	Coleoptera e	Col e	2	0 - 1	1.3	0.1	0	0 - 0	0.0	0.0
	Coleoptera f	Col f	1	0 - 1	0.6	0.0	0	0 - 0	0.0	0.0
	Staphylinidae b	Staph	5	0 - 2	2.5	0.2	0	0 - 0	0.0	0.0
Hemiptera	Cicacidae	Cica	3	0 - 2	1.3	0.1	0	0 - 0	0.0	0.0
Hymenoptera	Apocrita b	Apo b	1	0 - 1	0.6	0.0	0	0 - 0	0.0	0.0
	Apocrita c	Apo c	10	0 - 2	5.7	0.4	0	0 - 0	0.0	0.0
	Hymenoptera	Hyme	14	0 - 2	7.6	0.5	0	0 - 0	0.0	0.0
Orthoptera	Orthoptera a	Ortho a	33	0 - 5	12.0	1.2	0	0 - 0	0.0	0.0
	Orthoptera b	Ortho b	12	0 - 3	4.4	0.4	0	0 - 0	0.0	0.0
	Orthoptera c	Ortho c	2	0 - 1	1.3	0.1	0	0 - 0	0.0	0.0
Pseudoscorpionida		Pseud	1	0 - 1	0.6	0.0	0	0 - 0	0.0	0.0
Thysanoptera		Thysa	9	0 - 2	4.4	0.3	0	0 - 0	0.0	0.0
Exclusive to quadrat samples										

			Pitfall-traps				Quadrats			
Taxa		Abbrev	Sum	Min-Max	Occ	%	Sum	Min-	Occ	%
Araneae	Araneae c	Ara c	0	0 - 0	0.0	0.0	1	0 - 1	1.1	0.6
	Araneae f	Ara f	0	0 - 0	0.0	0.0	1	0 - 1	1.1	0.6
Hemiptera	Aphididae	Aphid	0	0 - 0	0.0	0.0	1	0 - 1	1.1	0.6
Hymenoptera	Apocrita a	Apo a	0	0 - 0	0.0	0.0	1	0 - 1	1.1	0.6
Oligocheata		Oligo	0	0 - 0	0.0	0.0	10	0 - 2	8.9	6.1

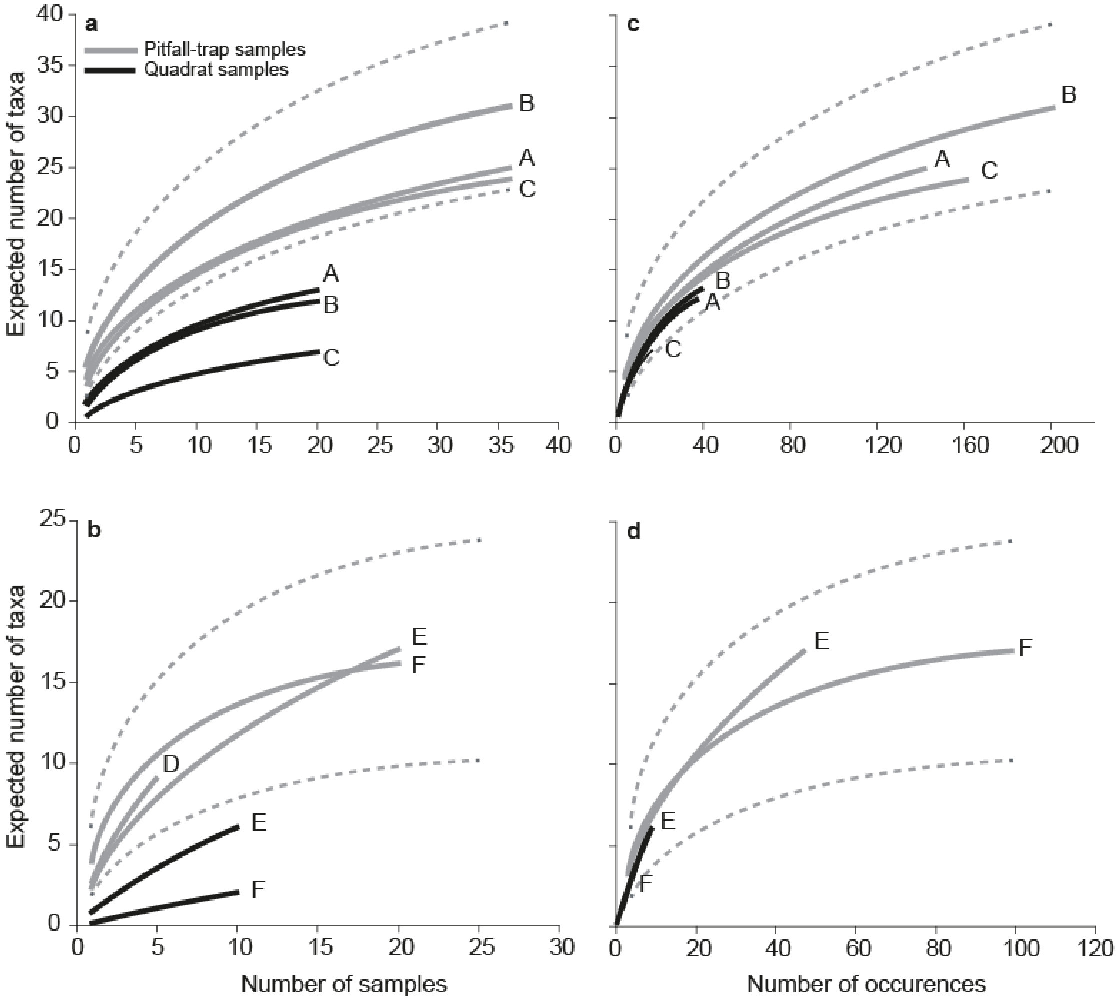

Figure 2. Rarefaction curves for invertebrate sampling methods in the Selwyn River (sites A, B, and C) and Lower Farm Stream (sites D, E and F) scaled to a, b the number of samples and c, d the number of occurrences. Dotted lines: 95% CI. For clarity, 95% CIs are shown only for pitfall traps at sites B an F. Widths of CIs are similar for the other method and other sites

Detection biases

The proportion of taxa exclusive to pitfall-trap samples was higher than the proportion exclusive to quadrat samples (Wilcoxon paired-sample test, $P < 0.05$, Figure 3). On average, 81 ± 14% (mean ± SD, n = 6) of the taxa were exclusive to pitfall traps, 4 ± 4% were exclusive to quadrat samples, and 4 ± 2% were shared by the two methods. Most of the taxa exclusive to pitfall-trap samples were Coleoptera, Araneae, Hymenoptera, Orthoptera, Pseudoscorpionida and Thysanoptera. The taxa exclusive to quadrat samples were Oligochaeta, Aphididae (Hemiptera), one Apocrita (Hymenoptera) morphospecies, and one Araneae morphospecies (Table 1). In addition, the ratio of singletons to exclusive taxa differed significantly between methods (Wilcoxon paired-sample test, $P = 0.01$). On average, singletons represented half of the taxa exclusive to pitfall-trap samples while 70% of the taxa exclusive to quadrat samples were singletons (Figure 3). Among shared taxa, only one was a singleton in a pitfall-trap sample (Hemiptera a), and ~50% were singletons in quadrat samples. Singletons in pitfall-trap samples were mostly Coleoptera and Hemiptera and singletons in quadrat samples were mostly Araneae, Hemiptera, and Hymenoptera

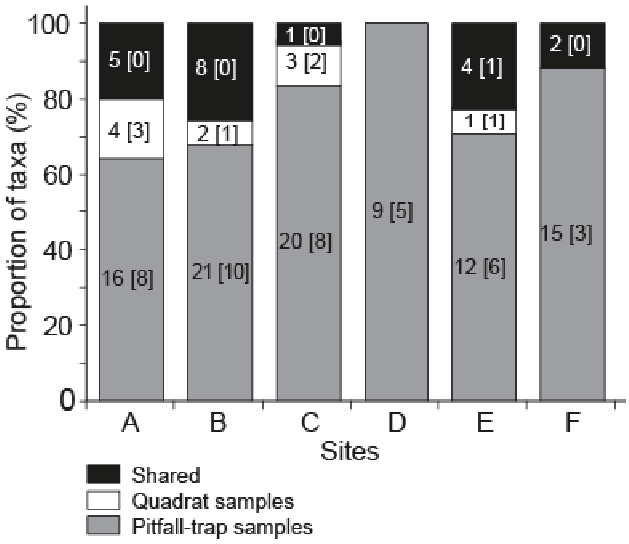

Figure 3. Proportions and numbers (written in bars) of taxa exclusive to pitfall-trap samples quadrat samples, and shared by the two methods at each site. The number of singletons is given in brackets

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Among-site differences in taxonomic richness and assemblage composition

There were no detectable differences in the expected number of taxa among the sites at the Selwyn River and Lower Farm Stream, as indicated by the overlaps of the 95% CIs for rarefaction curves for pitfall trap and quadrat samples (Figure 2).

Invertebrate composition in pitfall-trap samples differed significantly between sites at both rivers **(**Figure 4a, b, Stress value = 0.20 and 0.16; Global R = 0.43 and 0.27, $P < 0.001$, respectively). Sites A and D (dry for 1 day) and sites C and F (dry for > 1 month) were located on opposite sides of axis 1, and sites B and E were at intermediate positions (Figure 4a, b). The composition of invertebrates in quadrat samples differed significantly between sites in the Selwyn River (Figure 4c, Stress value = 0.16, Global R = 0.26, $P < 0.001$), but not in Lower Farm Stream (Figure 4d, Stress value = 0; Global R = 0.02, $P = 0.52$). Between-site differences in the composition of quadrat samples from the Selwyn River were less distinct than between-site differences in the composition of pitfall-trap samples; quadrat samples mostly differentiated invertebrate composition of site A samples from site B and C samples (Figure 4c). The most abundant taxa in pitfall-trap samples from the Selwyn River were Coccinelidae (Coleoptera), Miridae (Hemiptera), and Coleoptera b at site A and Orthoptera, Coleoptera d, and Cicacidae (Hemiptera) at site C (Figure 4a). The most abundant taxa in quadrats samples from the Selwyn River were Chilopoda, Myrmicidae (Hymenoptera), and Salticidae a (Araneae) at site A and Oligochaeta, Megaloptera, and Staphylinidae a (Coleoptera) at sites B and C (Figure 4c). At Lower Farm Stream, the most abundant taxa in pitfall-traps samples were Carabidae a (Coleoptera), Araneae d and Apocrita b (Hymenoptera) at site D and Pseudoscorpionides, Apocrita c (Hymenoptera), and Orthoptera at site F (Figure 4b). The number of taxa and individuals were too low in quadrat samples from Lower Farm Stream to detect between-site differences in invertebrate composition (Figure 4d).

Sampling completeness

Pitfall-trap and quadrat rarefaction curves did not reach plateaus, indicating that more collecting samples would have resulted in a substantial increase in taxa (Figure 2). Rarefaction curves for pitfall-trap samples had a greater tendency to level-off than rarefaction curves for quadrat samples, notably at the Lower Farm Stream sites (Figure 2c, d). The rate of taxa accumulation for both methods gradually decreased above 10 samples. For both methods, 67 to 84% of the maximum expected number of taxa (S_m) was collected within the first ten samples (Table 2). The last 10 pitfall-trap samples contained two to six additional taxa, and the last 10 quadrat samples contained one to four additional taxa. The percentage of the maximum estimated number of taxa (S_{est}) was higher for pitfall-trap samples than for quadrat samples. Only 50 to 70% of S_{est} was collected in 10 samples for both pitfall traps and quadrats, and 15 to 20 samples were required to collect 70 to 85% of S_{est} in the sampled areas of 180 m^2 (Table 2).

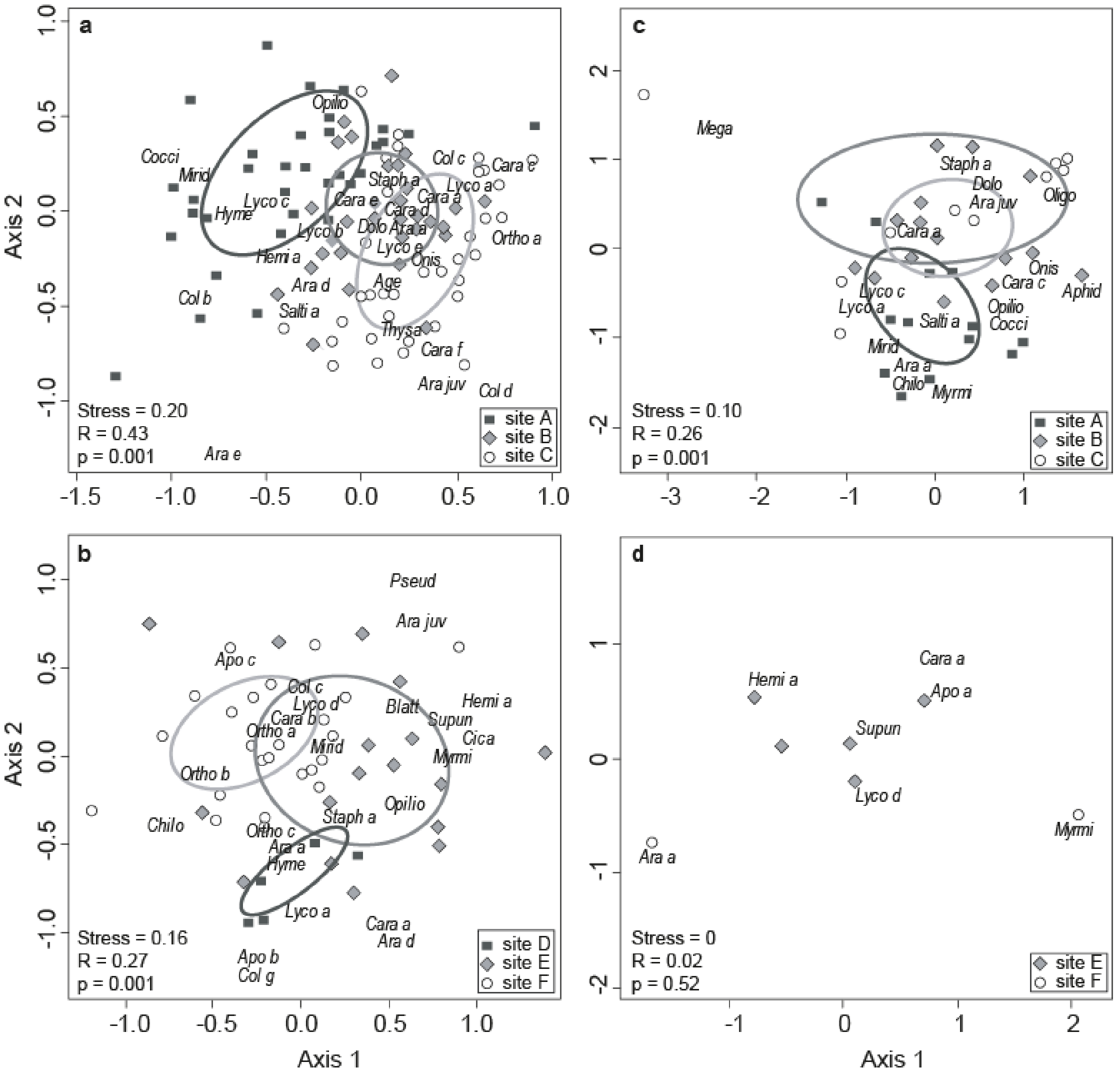

Figure 4 NMDS plots showing sites and invertebrate scores based on invertebrate assemblage dissimilarity in the Selwyn River and Lower Farm Stream a, b using pitfall traps and c, d quadrats. Dispersion ellipses represent standard deviation of site scores; See Table 1 for taxon codes. NMDS stress values and ANOSIM statistics (R and *p*) are indicated

DISCUSSION

Method comparisons

Our results indicate that pitfall-trapping produce a more precise estimate of taxonomic richness and assemblage composition than quadrat sampling in the studied dry riverbeds. Pitfall-trap samples contained more taxa than quadrat samples, the number of taxa increased more rapidly with increasing numbers of pitfall-trap samples compared with quadrat samples. Most of the taxa in pitfall-trap samples were not in quadrat samples, and most of the taxa in quadrat samples were also in pitfall-trap samples. There are three possible reasons for the methodological differences we observed.

First, the absence of vegetation at the sampling sites may have contributed to the higher sampling efficiency of pitfall traps compared to quadrat samples for an identical amount of time spent to collect and process samples. In previous comparisons, pitfall traps have proven to be more efficient and to produce more complete estimates of taxonomic richness in structurally simple habitats, such as sparsely vegetated grasslands or coastal dunes, than in densely vegetated habitats, because plants did not impede invertebrate movements (Schirmel *et al.*, 2010; Tista & Fiedler, 2011). In densely vegetated habitats, quadrat searches and other hand-collection methods have proven to be more efficient than pitfall traps (Uetz & Unzicker, 1976; Mesibov *et al.*, 1995). It is likely that the scarcity or absence of vegetation in dry riverbeds favors the movement of ground-dwelling invertebrates and increases the sampling efficiency and completeness of pitfall traps. The absence of vegetation may also reduce detection bias by reducing the number of taxa that avoid pitfall traps by moving through vegetation (Honěk, 1988; Melbourne, 1999). Not all dry riverbeds are unvegetated, however (*e.g.* Dieterich & Anderson, 1998; Jacobson *et al.*, 1999). In dry, vegetated riverbeds, quadrat sampling or other methods, or combinations of two or more methods may be more efficient than pitfall trapping alone for collecting terrestrial invertebrates.

Second, we considered a large range of taxa in this study, instead of focusing on particular groups (*e.g.* ants, ground beetles). Pitfall traps generally collect active invertebrates, such as spiders and Hymenoptera (Standen, 2000), while quadrat samples are more appropriate for slow-moving taxa, such as Diplopoda, some Carabidae, and Oligochaeta (Andersen, 1995; Mesibov *et al.*, 1995). In our study, most of invertebrates appeared to be relatively fast-moving taxa, and were more likely to be found in pitfall traps than in quadrats (Morill *et al.*, 1990). In some cases, sampling efficiency in quadrats can be increased by pouring water onto the soil to submerge and retain invertebrates (Desender & Segers, 1985). This is ineffective in gravel-bed rivers because of high sediment permeability and rapid drainage.

Third, diel movements of terrestrial invertebrates in and out dry riverbeds may have contributed to the observed differences between pitfall-trap and quadrat samples. Dry riverbeds can be harsh habitats for invertebrates during the day, due to low sediment moisture and high temperatures and solar radiation levels (Kassas & Imam, 1954; Steward *et al.*, 2011; Datry *et al.*, 2012) To avoid these conditions, some invertebrates may limit their use of dry riverbed to nighttime periods with lower temperatures and higher water availability (Broza, 1979). Similar diel activity patterns have been observed among ground-dwelling invertebrates of other arid environments (Cloudsley-Thompson, 2001). Diel activity patterns may be a source of detection bias, particularly for quadrat samples that are not collected continuously, and which under-sample nocturnal or diurnal taxa, depending on sampling period. This may explain in our study the large proportion of the 0.25 m^2 quadrat samples containing no individual, whereas others studies in gravel bars of rivers did not encounter such low abundances in quadrat samples of an identical size (Paetzold *et al.* 2008). To identify these biases and improve invertebrate sampling procedures for dry riverbeds, methodological comparisons need to be expanded to include sampling periods.

Sampling effort required

The sampling effort expended on estimates of taxonomic richness should be commensurate with the objectives of a study. If a study is intended to compile a complete or near-complete species inventory, the sampling effort must be high enough to ensure that the rarest taxa are collected (Delabie *et al.*, 2000). In the 180-m^2 grids sampled in our study, more than 30 pitfall-trap samples / 100 m^2 and 60 quadrat samples / 100 m^2 were probably needed to accurately estimate the total number of ground-dwelling invertebrate taxa. The large number of samples required for a complete inventory in our study indicates that some taxa that were present at the two riverbeds were not collected by pitfall-trapping and quadrat sampling. If sample number requirement that we estimated applies to other dry riverbeds, it is likely that too few samples were collected in previous studies aiming to characterize ground-dwelling invertebrate fauna in dry riverbeds in South Africa (Wishart, 2000), Australia and Italy (Steward *et al.*, 2011). These observations suggest that the taxonomic richness of ground-dwelling invertebrates has been underestimated in each case and not the least when the time during which pitfall traps were deployed was smaller than in our study (Schirmel *et al.*, 2010). Since a much smaller number of samples may contain 70 to 80% of the total number of taxa, then the maximum taxonomic richness reported in South Africa (327 taxa; Wishart, 2000), Australia and Italy (320 taxa; Steward *et al.*, 2011), and New Zealand (51 taxa as morphospecies; present study) underestimated from 20 to 30% the total number of taxa.

In a context of management and conservation, a compromise is often necessary between the sampling completeness and the experimental constraints of time and finance (Obrtel, 1971). Such a compromise can be reached by making the number of samples match precisely the study objectives. For example, if a study intents to examine the factors driving species richness and composition, the number of samples can be reduced to focus on the most common taxa only and collecting 70-80% of the estimated total number of taxa is usually sufficient (Delabie *et al.*, 2000; Baselga & Novoa, 2006). In the 180-m^2 grids sampled in our study, the use of the pitfall-trap method and the collection of eight to eleven samples / 100 m^2 was sufficient for collecting 70 to 80% of the estimated total number of taxa. Such reduction of the sampling effort can be of high importance in habitats with poorly known invertebrate assemblages such as dry riverbeds, since a cost-effective method can help to facilitate and stimulate researches. More generally, we believe the findings of this study may also apply to similar environments, such as rocky deserts, unvegetated banks and bars of rivers, and varial zones of ponds and lakes.

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4

CARACTERISATION DES COMMUNAUTES D’INVERTEBRES TERRESTRES DES LITS ASSECHES

Article 2

Organization of terrestrial arthropods along lateral and longitudinal aquatic-terrestrial gradients in two temporary rivers with contrasted climatic conditions

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En preparation

ABSTRACT

1. In temporary rivers and their adjacent riparian zones, habitats alternate between aquatic and terrestrial conditions along lateral and longitudinal dimensions. Whereas much attention has been given to aquatic communities, how terrestrial arthropods are organized in these two dimensions remains poorly understood. Compared to riparian zones, dry riverbeds are harsh habitats. Moreover, environmental conditions (e.g. sediment moisture, vegetation cover) vary along dry riverbeds as a result of lateral and longitudinal gradients in drying duration and frequency. We predicted terrestrial arthropod assemblages i. to differ between dry riverbeds and riparian zone and ii. to be structured longitudinally along river channels owing to lateral and longitudinal variations in environmental conditions along aquatic-terrestrial gradients. In this study, we examined the composition of terrestrial arthropod assemblages before and during a dry period in the dry riverbeds and riparian zones of two temporary rivers from France located in contrasted climatic regions. In both rivers, assemblage composition differed only slightly laterally, indicating a strong contribution of riparian taxa to dry riverbed assemblages. Longitudinal compositional variations were low, indicating that local variations in environmental conditions (e.g. temperature, soil moisture) and species dispersal were the primary drivers of terrestrial arthropod distribution in the longitudinal dimension. While longitudinal structures are common features of riverine ecosystems, such structures seem not to exist for terrestrial arthropods. Rather, a lateral source-sink dynamic appeared to be the dominant mechanism by which assemblages are organized in temporary rivers.

Key-words: aquatic-terrestrial ecotone, riparian zone, dry riverbed, intermittent rivers, beta diversity

INTRODUCTION

Temporary rivers, these rivers that periodically cease to flow, are increasingly viewed as coupled terrestrial and aquatic ecosystems (Larned *et al.* 2010). Alternating drying-rewetting cycles in the riverbeds and their adjacent riparian zones create lateral and longitudinal gradients along which habitats shift from aquatic to terrestrial conditions (Stanley *et al.* 1997; Doering *et al.* 2007, Datry *et al.* 2012). Drying duration and frequency vary laterally across river channels with the transverse elevation gradient (Junk *et al.* 1989; Gregory *et al.* 1991; Benke *et al.* 2000) and longitudinally with the progressive extension of the dry reach in the upstream or downstream direction during drying phases (Larned *et al.* 2011; Datry *et al.* 2012). These aquatic-terrestrial gradients have been shown to shape aquatic communities in temporary rivers (Boulton & Lake 1992, Paltridge *et al.* 1997; Fritz & Dodds 2004, Datry 2012, Datry *et al.* 2012) and are most likely also strong determinants of terrestrial communities. However, in spite numerous and diverse terrestrial arthropods colonized dry riverbeds (Andre *et al.* 1997; Wishart 2000, Steward *et al.* 2011, Datry *et al.* 2012, McCluney & Sabo 2012), very little is known on their organization along the lateral and longitudinal aquatic-terrestrial gradients.

Riparian zones represent a probable source of colonizers for dry riverbeds due to their immediate proximity and rich biodiversity (Sabo *et al.* 2005, Steward *et al.* 2011). However, dry riverbeds differ quite substantially from riparian zones, as environmental conditions gradually change along lateral aquatic-terrestrial gradients. Indeed, exposed sand and gravel in riverbeds are harsh environments (Tockner *et al.* 2009), whereas riparian zones provide more benign environmental conditions (Tockner & Stanford 2002). For example, the distribution of the vegetation is typically zonated laterally across river channels, reflecting the relative tolerances of species to stream hydraulic conditions and water stress (Salo *et al.* 1986). Dry riverbeds display low plant diversity and a sparse vegetation cover (Stromberg *et al.* 2009; Katz *et al.* 2012). Consequently, diel variations in light and temperature are more contrasted in dry riverbeds compared to riparian areas, and temperature can be as up as 60°C (Hall & Harcombe 1998, Steward *et al.* 2011). Dry riverbeds also hold a lower capacity to retain soil moisture compared to riparian areas, due to coarser sediments (Kassas & Girgis 1964, Datry *et al.* 2012). These environmental factors are known to influence the distribution of terrestrial arthropods in riparian zones of perennial rivers (Antvogel & Bonn 2001, Bates *et al.* 2007, Lambeets *et al.* 2010) and their lateral organization in temporary rivers during dry periods could lead to different arthropod assemblages between dry riverbeds and riparian zones. Notably, dry riverbeds could be not suitable habitats for some riparian species and pioneer terrestrial species with adaptations to harsh environments could also move from upland habitats into dry riverbeds and constitute an additional source of dry riverbed colonists.

Longitudinal structures are common features of riverine ecosystems (Vannote *et al.* 1980, Thorp *et al.* 2006). As for benthic and hyporheic invertebrates (Arscott *et al.* 2010, Datry *et al.* 2007, Datry 2012), fish (Davey & Kelly 2007) or plant (Stromberg *et al.* 2009) biodiversity patterns, terrestrial arthropod communities are likely organized longitudinally along temporary rivers during dry periods, due to the existence of longitudinal aquatic-terrestrial gradients. Indeed, the upstream or downstream expansion of the dry reaches generates longitudinal gradients of dry period duration which induce longitudinal variations in soil moisture, plant species composition, organic matter accumulation and decomposition rates (Stromberg *et al.* 2009; Corti *et al.* 2011, Datry *et al.* 2012, Katz *et al.* 2012). Sites having been dried for long periods may display different arthropod species than sites that have been just drying, due to the elimination of water-sensitive species (Andersen *et al.* 1986; Greenwood & McIntosh 2010) and the growing complexity of assemblage structure with time (Larned *et al.* 2010) Conversely, if adjacent riparian zones are the major sources of colonists for dry riverbed habitats, such longitudinal structures could be weaker for terrestrial arthropods than for other biological groups.

In this study, we examined dry riverbed and riparian terrestrial arthropods from two temporary rivers of south-eastern France located in contrasted climatic areas. We collected terrestrial arthropods using pitfall traps at five sites in the riparian zone before a seasonal summer dry period and during summer both in the riparian zone and the dry riverbed We predicted that terrestrial arthropod assemblages of dry riverbeds i. would differ from those of riparian zones and ii. would show strong longitudinal structures due to variations in environmental conditions (e.g. light intensity, sediment moisture) along lateral and longitudinal aquatic-terrestrial gradients.

METHOD

Study sites

The study was conducted between 2010 and 2011 in the Albarine and Asse rivers, two alluvial, gravel-bed temporary rivers of south-eastern France. The two rivers are located in two contrasted climatic regions and have different hydrological and geomorphological dynamics.

The Albarine River drains a 313 km^2 catchment in eastern France (**Figure 1**) and has a mean annual discharge of 6.88 $m^3.s^{-1}$ (Datry *et al.* 2011). The regional climate is temperate and broadly characterized by wet winters and warm, dry summers. The Asse River is a braided river with a complex channel network that drains a 657 km^2 catchment in the southeastern France and has a mean annual discharge of 5.0 $m^3.s^{-1}$ (Mano *et al.* 2009) (**Figure 1**). The regional climate is Mediterranean, broadly characterized by mild to cool, wet winters and warm to hot, dry summers. Average annual precipitation range from 1000 to 1200 mm per year at the Albarine River and from 600 to 800 mm per year at the Asse.

The downstream sections of the Albarine and Asse Rivers flow across alluvial plains before joining the Ain and the Durance rivers, respectively (**Figure 1**). At the Albarine River, drying occur along the alluvial plain due to seepage into the underlying aquifer (Datry *et al.* 2011). River drying starts at the confluence with the Ain River during low runoff period and gradually extends upstream over a 10 km-long temporary section. At the Asse River, drying occurs in the alluvial plain at two 3-km-long temporary sections spaced 7-km apart, due to the combined effects of seepage into the underlying aquifer, groundwater abstraction in the floodplain for agriculture, and bed aggradation (Datry *et al. in review*). At the Albarine River, long dry periods of 4 to 5 months occur each year in early summer until autumn (Datry *et al.* 2011). The two temporary sections at the Asse River dry on average from 4 to 6 weeks annually, during late summer (Datry *et al. in review*).

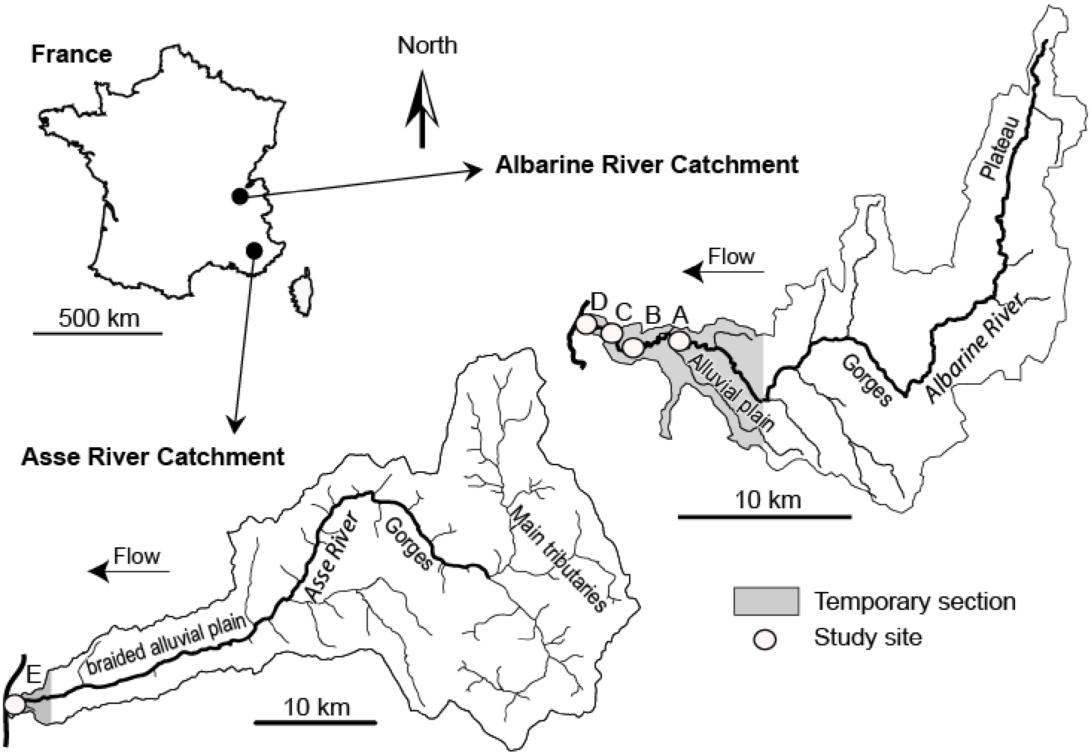

Figure 1 Location of the Albarine and Asse river catchments, showing the temporary sections and the study sites

Four sites along the temporary section of the Albarine River (A to D, **Figure 1**) and one site in the most downstream temporary reach of the Asse River (E, **Figure 1**) were sampled for terrestrial arthropods. Sites A to D were scattered 2 to 4-km apart along the 10-km long temporary section of the Albarine River (**Figure 1**). Length of each site was defined as 10x the mean width of the active channel to account for heterogeneity of microhabitat types (e.g. gravel and sand bars, deep holes, accumulation of woody debris) and allow among-site comparisons. We defined the active channel as the area constituted of inundated and exposed riverbed sediments between established edges of perennial, terrestrial vegetation and abrupt changes in slope. The width of the active channel was of ~18m on average at sites A to D and ~110m at site E. The active channel at the Albarine River was bordered by a riparian forest dominated by *Populus sp.*, *Alnus glutinosa* and *Fraxinus excelsior* trees. At site E, riparian vegetation around the active channel was distinguished by shrubs and trees dominated by *Salix sp.*, *Populus tremula*, *Populus nigra*, and *Alnus incana*.

Sampling design

Sites were sampled for terrestrial arthropods using pitfall traps (Spence and Niemela 1994, Corti *et al. in revision*). Sites A to D were sampled four times at two month intervals during two sampling periods; twice before all the sites dried (April and June 2010) and twice while all the sites were dry (August and October 2010). At site E, arthropods were sampled five times at three-week intervals during two sampling periods; three times before the site dried (June, July and August 2011) and twice while the site was dry. At the two rivers, once a site dried, it stayed dry with no partial reestablishment of flow between consecutive sampling dates.

Pitfall traps were installed at least three meters apart along transects crossing the active channel perpendicularly to flow direction (**Figure 2**). We defined three transects offset from each other by 40m at sites A to D and five transects offset from each other by 200m at site E. Transect length corresponded to 2x the wetted-width of the riverbed measured at base flow condition. The average width of the wetted riverbed was of 15m at the Albarine River and 8m at the Asse River. Before the dry period, we installed two pitfall traps on each side of the wetted riverbed at each transect: one at the transect extremity and one from 0.2 to 0.5m to the waterline. Two to three additional pitfall traps were installed in the riverbed during the dry period at each transect, depending on the width of the wetted riverbed before the dry period. When two channels were present at the Asse River, the procedure was repeated on each channel (**Figure 2**).

Pitfall traps consisted of 7-cm tall, 8-cm diameter plastic containers inserted in sediments until flush with the riverbed surface. Ethylene glycol (15 ml) was added to each container as a preservative, and the containers were covered with a 15-cm diameter plastic plate to keep rain out. All pitfall traps were deployed for 7 days after which the contents were transferred to plastic bags and stored until analysis. The ethylene glycol served as a sample preservative.

Samples were groups on the basis of the sampling period and the habitat type into which pitfall traps were installed, i.e. 1) in the riparian zone before the dry period (RZ-B), 2) in the riparian zone during the dry period (RZ-D), and 3) in the dry riverbed (DRB). A total of 67 arthropod samples (15%) were lost due to disturbance by digging mammals (e.g. Wild boar), small rain events, rising groundwater or improper handling. In total, 370 arthropod samples were collected, including 241 samples from the Albarine River and 129 samples from the Asse River (**Table 1**).

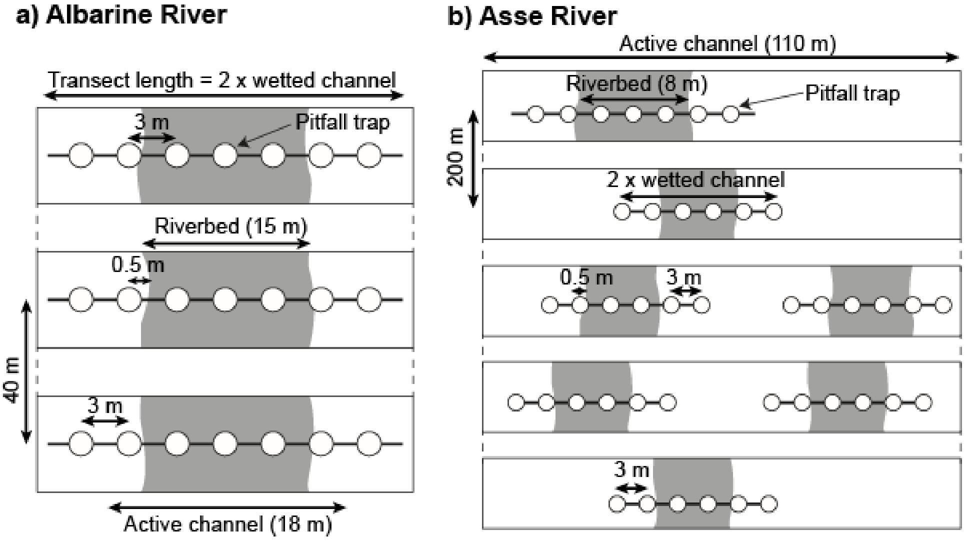

Figure 2 Schematic representation of the scattering of pitfall traps along transects at the Albarine River (a) and Asse River (b). Pitfall traps (white circles) were scattered at least 3-m apart along transect which the length depended on the width of the wetted riverbed. Pitfall traps in the riverbed were positioned only during the dry period.

Table 1 Number of samples collected on the number of samples installed along transects at sampling sites in RZ-B, RZ-B, and DRB.

	A	B	C	D	E	Total
RZ-B	24/24	24/24	24/24	23/24	63/84	158/180
RZ-D	20/24	23/24	22/24	21/24	43/56	129/152
DRB	10/18	14/18	17/18	16/18	23/30	80/102
Total	54/66	61/66	63/66	60/66	129/170	367/434

Laboratory procedures

Invertebrates from pitfall traps were rinsed with tap water above a 63-µm mesh sieve and the retained material was preserved in 70% ethanol. We identified arthropods from pitfall-trap samples to the lowest practical taxonomic level - species or genus for most Coleoptera, Aranea, and Formicidae, and family, class, or order for other taxa. Species identifications were made by the authors and numerous collaborators (see section 'Acknowledgments'), using published keys and reference collections (e.g. du Chatenet 2005). Species were named according to the nomenclature of the Fauna Europaea Web Service (2012). Collembola, Acarina, and aerial taxa (e.g., Diptera, Apidae, and Lepidoptera) were not included in data analyses as pitfall traps are not an appropriate sampling method for these taxa (Yi *et al.* 2012, Corti *et al. in revision*). Immature spiders and larvae were also removed from the dataset as accurate identifications were not possible. Overall, 55% of individuals were determined to species level, 15% to genus or sub-family level and 30% to family, order or class.

All arthropods were assigned to predator/polyphagous, phytophagous or detritivorous feeding guilds. The predator/polyphagous guild included species which opportunistically consume organic matter, live preys or carrions. Designation to these feeding guilds was derived from existing literature (e.g. Hering & Plachter 1997; Rykken *et al.* 2007) and general knowledge. Aleocharinae (Coleoptera) taxon consisted in several species belonging to diverse feeding guilds and consequently was not included in feeding guild analysis (see 'data analysis' section)

Data analysis

Lateral variation in taxonomic richness

Taxonomic richness estimates are sensitive to the number of samples collected (Colwell *et al.* 1994). Therefore, the rarefaction method (*sensu* Gotelli & Colwell 2001) was used to assess differences in taxonomic richness among RZ-B, RZ-B, and DRB. Rarefaction standardizes the sampling effort through random sub-sampling of a dataset and provides the expected taxonomic richness in a given number of samples (Gotelli & Colwell 2001).

Lateral variation in assemblage composition

We used the Bray-Curtis dissimilarity index to compare arthropod assemblage composition among RZ-B, RZ-B, and DRB. Patterns of dissimilarity were analyzed using non-parametric, non-metric multidimensional scaling (NMDS). A permutational multivariate analysis of variance called ADONIS (Anderson 2001) was used to test for differences in assemblage composition among RZ-B, RZ-B, and DRB. ADONIS returns a statistic R^2, which is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation), and a p-value estimated by repeated permutations of the data (Anderson 2001).

NMDS and the ADONIS analysis were run with arthropod abundance data, after removal of taxa < 0.1 % of individuals, to minimize the influence of rare or inadequately sampled taxa. Data were square-root-transformed and double-standardized (Wisconsin method), by standardizing taxa by their maxima, and then standardizing samples by sample totals (Oksanen *et al.* 2012).

Habitat preference for the riparian zone and the dry riverbed

We assessed habitats preferences of terrestrial arthropods for RZ-B, RZ-D and DRB by conducting an Indicator Species analysis (INDVAL) (Dufrêne & Legendre 1997). INDVAL calculates an indicator value for each taxon by combining information about species relative abundance and relative frequency of occurrence. An indicator value of 100% indicates that all individuals of a taxon were found exclusively in a group, and that this taxon was collected in all samples from that group. Indicator values were tested for statistical significance using Monte-Carlo procedures (1000 permutations). We first ran INDVAL analysis within each site using the entire dataset to assess both temporal and spatial preferences for the RZ-B, the RZ-D or the DRB. Next, we ran a second INDVAL analysis using only RZ-D and DRB samples to identify habitat preference of taxa only during the dry period. We assumed that a species showed preference for the RZ-B, the RZ-D or the DRB if the indicator value was > 20%.

Lateral variation in feeding guild organization

We compared the composition of arthropod assemblages among RZ-B, RZ-B, and DRB by calculating the relative abundance of predator/phytophagous, detritivorous and polyphagous arthropods.

Beta diversity along the dry reach of the Albarine River

We assessed the structures of arthropod assemblages along the dry reach of the Albarine River by assessing compositional variations (Beta diversity) across three hierarchical levels of spatial scales, i.e. among samples within transects, among transects within sites and among sites within the Albarine River. We estimate beta diversity at each spatial scale through an additive partitioning of taxonomic richness into alpha (α) and beta (β) diversity components (Lande 1996; Crist *et al.* 2003), with $\gamma = \alpha + \beta 1 + \beta 2 + \beta 3$. Gamma diversity ($\gamma$) refers to the total taxonomic richness of arthropods in DRB, α refers to the average taxonomic richness in samples, and β refer to compositional variations within each hierarchical level ($\beta 1$ = among samples within transects, β2 = among transects within sites and β3 = among sites within the Albarine River). The observed diversity components were compared at all hierarchical levels with a null distribution of individuals generated by individual-based randomizations, to calculate expected diversity components and to test the significance of observed patterns of diversity (Crist *et al.* 2003). The *p*-values estimated by this procedure indicate the probably of obtaining a diversity value as large as (or as small as) it could be expected by chance. Separate diversity partitioning analysis were applied 1) to the entire arthropod assemblage, 2) to the assemblage of taxa representing more than 0.3% of individuals, and 3) to the assemblage of taxa representing less to 0.1% of individuals, in order to evaluate whether similar results were obtained with common and rare taxa.

All statistical analyses were carried out using R software (R Development Core Team 2012) and functions in the package Vegan (Oksanen *et al.* 2012) and Labdsv (Roberts 2012). For rarefaction curves, differences among sampling groups were considered statistically significant if CIs did not overlap. For other statistical analysis, $p < 0.05$ was used to indicate statistical significance.

RESULTS

We identified a total of 298 taxa, including 241 taxa in the Albarine River and 84 taxa in the Asse River (**Supplementary material S1**). At the Albarine River, the 5 most frequent and abundant taxa were Oniscidea (Crustacea, 6.5% of occurrences), Aleocharinae (Coleoptera, 4.6%), *Myrmica Rubra* (Formicidae, 3.4%), Opiliones (2.9%) and *Lasius niger* (Formicidae, 2.6%). At the Asse River, the most frequent taxa were *Labidura riparia* (Dermaptera, 17.9%), *Pardosa Wagleri* (Aranea, 10.3%), Orthoptera (6.6%), and *Formica selysi* (Formicidae, 6.1%) and *Oedothorax apicatus* (Araneae, 4.0%). Sixty-five (26%) and 35 taxa (41%) at the Albarine and Asse Rivers, respectively, were collected in only one sample.

Lateral variation in taxonomic richness

Sample-based rarefaction curves showed that taxonomic richness in DRBs was lower compared to RZ-D at sites A and C and non-significantly different at sites B, D, and E (**Figure 3**). On average, taxonomic richness was 1.2 times lower in DRB (mean $\pm$ SD = 42.6 $\pm$ 12.5) than in RZ-D (47.8 $\pm$ 13.0) for a similar sampling effort in term of number of samples. By contrast, taxonomic richness strongly differed between the two sampling periods, as indicated by the absence of overlap of CIs (**Figure 3**). On average, taxonomic richness was 1.5 times higher in RZ-B (mean $\pm$ SD = 47.8 $\pm$ 13.0) than in RZ-D and DRB (42.6 $\pm$ 12.5) for a similar sampling effort in term of number of samples.

Lateral variation in assemblage composition

The composition of arthropod assemblages did not differ strongly among RZ-B, RZ-D and DRB (**Figure 4**). ADONIS revealed a low separation of sampling groups based on their assemblage composition at sites A, B and D, with R^2 value ranging from 0.12 to 0.16 and nearly no among-groups differences at site C and E (R^2 = 0.08 and 0.07 respectively) (**Table 2**). From 65 to 95 % of taxa collected in DRB were also collected in RZ-D and from 66 to 81 % of taxa collected in RZ-D and DRB were also collected in RZ-B. Compositional difference observed at site A, B and D was mostly due to differences between RZ-B and RZ-D on one side, and DRB on the other side (**Figure 4**). Higher relative abundances or occurrences of *Oedothorax apicatus* (Araneae), *Lasius niger* (Formicidae), *Aphidoidea*, *Zorochros dermestoides* (Coleoptera), and *Oedothorax retusus* (Araneae) in DRBs compared to the RZ-B and RZ-D contributed to the observed differences (**Figure 4**).

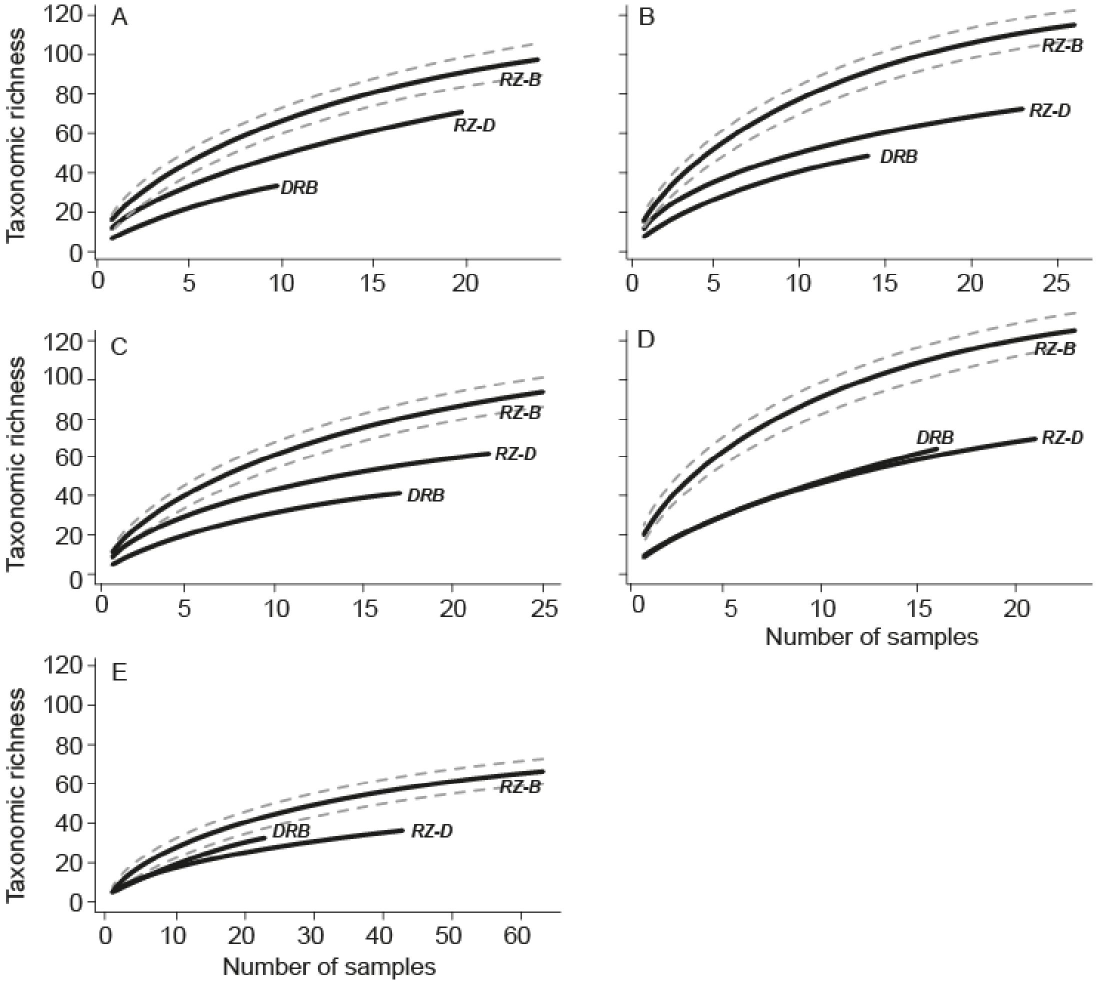

Figure 3 Rarefaction curves scaled to the number of samples for terrestrial arthropods collected in RZ-B, RZ-D and DRB. For clarity, 95% CIs (grey dotted lines) are shown only for the RZ-B. Widths of CIs are similar for RZ-B and DRB. Capital letters indicate site names.

Table 2. Parameters of the permutational multivariate analysis of variance (ADONIS) comparing the composition of arthropod assemblages in RZ-B, RZ-D and DRB at each site. The degree of freedom (d.f.), the *F*-test (F) and R² statistics, and their p-value (*p*) are shown.

	d.f.	F	R²	*P*
A	2, 52	4.66	0.15	0.001
B	2, 60	3.87	0.12	0.001
C	2, 60	2.65	0.08	0.001
D	2, 59	5.60	0.16	0.001
E	2, 128	5.00	0.07	0.001

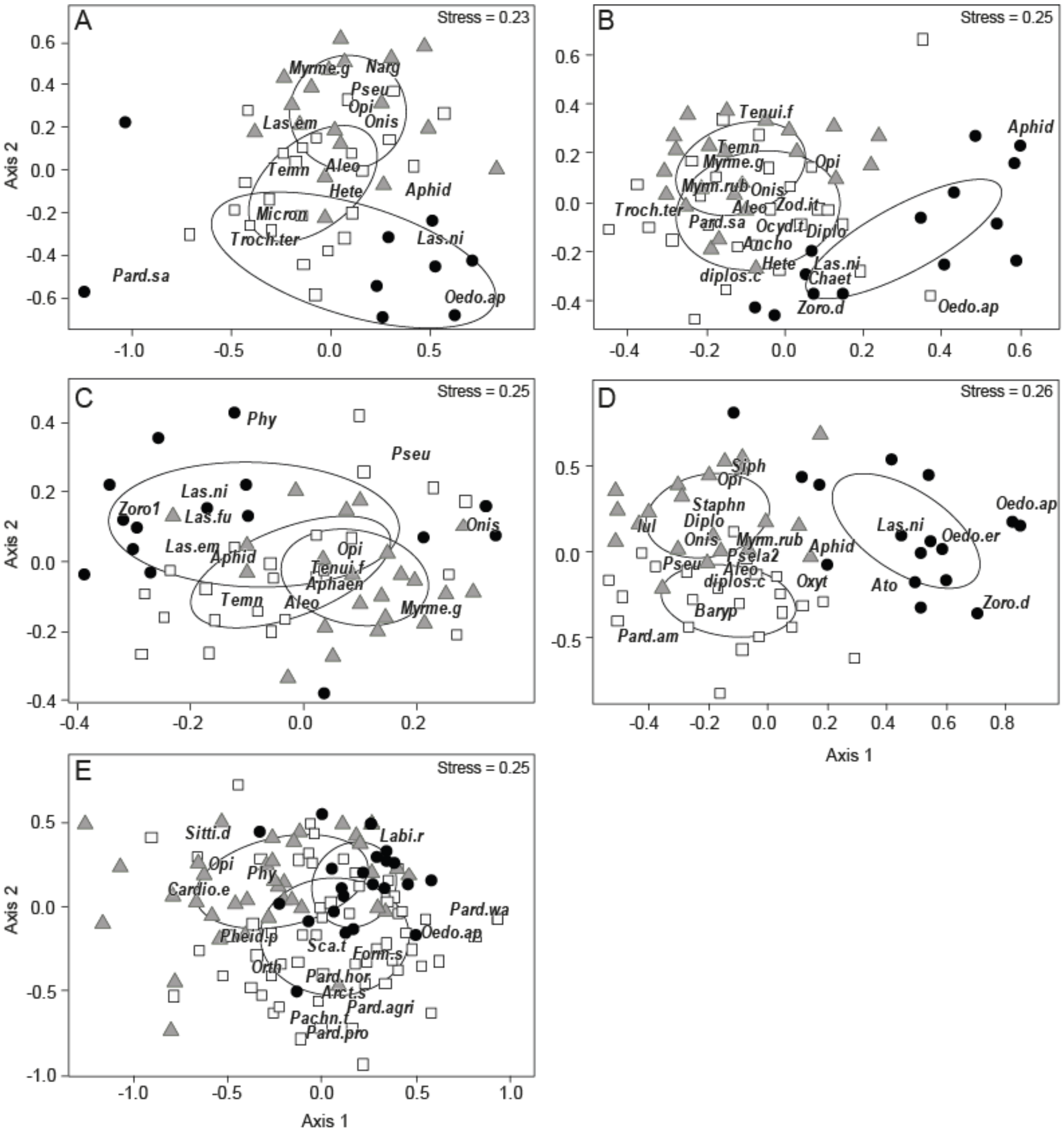

Figure 4 Two-dimensional NMDS plot showing the scores of samples and arthropods collected in RZ-B (White squares), in RZ-D (Grey triangles), and in DRB (Dark circles) at the five sampling sites (capital letters). Dispersion ellipses in black represent standard deviation of site scores of sampling groups. For clarity, only taxa representing more than 1% of individuals are shown. See supplemental material S1 for taxon codes.

Habitat preference for the riparian zone and the dry riverbed

INDVAL analysis indicated that from 4 to 12 taxa showed habitat preference for RZ-D or DRB (**Table 3**). Only 2 to 5 taxa showed habitat preference for DRB at each site. Among them, *Oedothorax apicatus* (Aranea), *Chaetocnema sp*. (Coleoptera), *Zorochros dermestoides* (Coleoptera) were collected at nearly all sites of the Albarine River and were not collected in RZ-D. Taxa showing habitat preference for DRB were also collected in RZ-B or RZ-D, in the same site or in another one. *Oedothotax retusus* (Araneae) was the only taxon with habitat preference for DRB that was collected exclusively in DRB. In addition, nearly all the taxa with habitat preference for RZ-D were also collected in RZ-B.

Table 3. Indicator values (%) for taxa in RZ-B, RZ-D, and DRB at the five sampling sites and all sites pooled together (All). Taxa with significantly higher indicator values in DRB are shown in bold type. Only taxa with indicator value > 0.20% in RZ-D and DRB and with $p < 0.05$ are shown. Permutation tests compared only RZ-D and DRB.

			Indicator values			
Site	Taxa	Code	RZ-B	RZ-D	DRB	*p*
A	Aleocharinae (Coleoptera)	Aleo	0.41	0.46	0.01	0.038
	Myrmecina graminicola (Formicidae)	Myrme.g	0.02	0.55	0.00	0.014
	***Oedothorax agrestis* (Araneae)**	**Oedo_ag**	**0.00**	**0.00**	**0.30**	**0.017**
	***Oedothorax apicatus* (Araneae)**	**Oedo_ap**	**0.00**	**0.00**	**0.70**	**0.001**
	Oniscidea	Onis	0.60	0.87	0.01	0.001
	Opiliones	Opi	0.05	0.70	0.01	0.007
	Temnothorax sp. (Formicidae)	Temn	0.24	0.45	0.00	0.019
B	***Chaetocnema sp*. (Coleoptera)**	**Chaet**	**0.11**	**0.00**	**0.29**	**0.013**
	Myrmica rubra (Formicidae)	Myrm.rub	0.22	0.72	0.00	0.001
	Myrmecina graminicola (Formicidae)	Myrme.g	0.08	0.35	0.00	0.025
	***Oedothorax apicatus* (Araneae)**	**Oedo_ap**	**0.00**	**0.00**	**0.43**	**0.002**
	***Oedothorax retusus* (Araneae)**	**Oedo_er**	**0.00**	**0.00**	**0.29**	**0.015**
	Oniscidea	Onis	0.43	0.92	0.01	0.001
	Pseudoscorpionida	Pseu	0.06	0.43	0.00	0.007
	Tenuiphantes flavipes (Araneae)	Tenui.f	0.13	0.35	0.00	0.035
C	*Aphaenogaster subterranea* (Formicidae)	Aphaen	0.04	0.42	0.01	0.016
	Diplocephalus cristatus	**Dipl.c**	**0.05**	**0.00**	**0.29**	**0.013**
	Myrmecina graminicola (Formicidae)	Myrme.g	0.08	0.64	0.00	0.001
	Oniscidea	Onis	0.26	0.74	0.04	0.001
	Tenuiphantes flavipes (Araneae)	Tenui.f	0.05	0.32	0.00	0.014
	***Zorochros dermestoides* (Coleoptera)**	**Zoro.d**	**0.00**	**0.00**	**0.29**	**0.011**
D	Aleocharinae (Coleoptera)	Aleo	0.53	0.47	0.05	0.029
	***Chaetocnema sp.* (Coleoptera)**	Chaet	0.00	0.00	0.38	0.005
	Diplopoda	Diplo	0.36	0.52	0.01	0.004
	Iulidae	Iul	0.20	0.33	0.00	0.025

Site	Taxa	Code	Indicator values RZ-B	 RZ-D	 DRB	*p*
	***Lasius niger* (Formicidae)**	**Las_ni**	**0.03**	**0.00**	**0.36**	**0.006**
	***Oedothorax apicatus* (Araneae)**	**Oedo_ap**	**0.00**	**0.00**	**0.56**	**0.001**
	***Oedothorax retusus* (Araneae)**	**Oedo_er**	**0.02**	**0.01**	**0.66**	**0.001**
	Oniscidea	Onis	0.40	0.70	0.07	0.005
	Pseudoscorpionida	Pseu	0.22	0.38	0.00	0.013
	Staphylininae	Staphn	0.15	0.38	0.00	0.012
	Trechus quadristriatus (Coleoptera)	Tre.q	0.02	0.29	0.00	0.033
	***Zorochros dermestoides* (Coleoptera)**	**Zoro.d**	**0.07**	**0.00**	**0.38**	**0.002**
E	***Labiduria riparia* (Dermaptera)**	**Labi.r**	**0.21**	**0.26**	**0.69**	**0.001**
	***Oedothorax apicatus* (Araneae)**	**Oedo_ap**	**0.13**	**0.01**	**0.21**	**0.036**
	Pardosa wagleri (Araneae)	**Pard_wa**	**0.34**	**0.03**	**0.69**	**0.001**
	Phyllotreta sp. (Coleoptera)	Phy	0.01	0.26	0.00	0.035
	Scarites terricola (Carabidae)	Sca.t	0.13	0.21	0.00	0.034
All	Aleocharinae (Coleoptera)	Aleo	0.25	0.26	0.04	0.011
	***Lasius niger* (Formicidae)**	**Las_ni**	**0.05**	**0.04**	**0.21**	**0.032**
	Myrmecina graminicola (Formicidae)	Myrme.g	0.03	0.27	0.00	0.001
	***Oedothorax apicatus* (Araneae)**	**Oedo_ap**	**0.01**	**0.00**	**0.38**	**0.001**
	***Oedothorax retusus* (Araneae)**	**Oedo_er**	**0.00**	**0.00**	**0.21**	**0.001**
	Oniscidea	Onis	0.25	0.55	0.02	0.001
	Opiliones	Opi	0.05	0.35	0.02	0.001
	***Pardosa wagleri* (Araneae)**	**Pard_wa**	**0.14**	**0.01**	**0.22**	**0.001**
	Pseudoscorpionida	Pseu	0.07	0.24	0.00	0.001
	***Zorochros dermestoides* (Coleoptera)**	**Zoro.d**	**0.02**	**0.00**	**0.22**	**0.001**

Lateral variation in feeding guild organization

The contribution of the different feeding guilds differed among RZ-B, RZ-D and DRB (**Figure 5**). Predator and polyphagous arthropods dominated in the DRB, comprising from 64 to 95% of arthropods and detritivorous arthropods were scarce, comprising from 3 to 9% of arthropods. The contribution of predator and polyphagous arthropods was on average 1.5 times higher in DRB compared to RZ-D, coinciding with a relative abundance of detritivorous arthropods on average 5 times lower in DRB compared to RZ-D. There was no strong difference in the composition of feeding guilds between RZ-B and RZ-D (**Figure 5**).

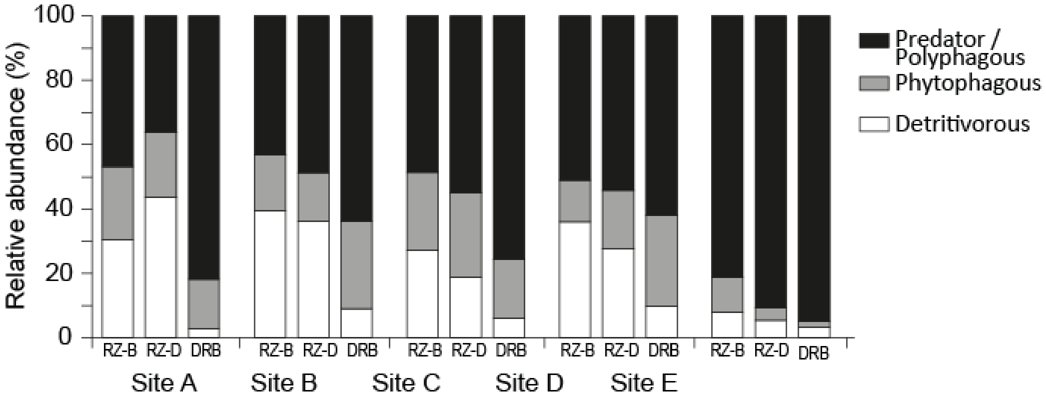

Figure 5 Relative abundance (%) of feeding guilds of terrestrial arthropods collected in RZ-B, RZ-D and DRB at the five sampling sites.

Beta diversity along the dry reach of the Albarine River

The additive partitioning of taxonomic richness in the dry riverbed of the Albarine River showed that beta diversity among sites within the river (i.e. β3) was always larger than expected by chance, indicating that among-site differences in assemblage composition contribute significantly to increase the total taxonomic richness along the dry riverbed (**Figure 6**). By contrast, α (i.e. average taxonomic richness in samples), β1 (i.e. diversity among samples within transects), and β2 (i.e. diversity among transects within sites) were always smaller or not significantly different than expected by chance. Among-sites differences in assemblage composition (β3) for the entire assemblage accounted for 55% of the total taxonomic richness. However, additive partitioning of taxonomic richness for common and rare taxa assemblages showed that β3 was largely influenced by the distribution of rare taxa across spatial scales. Among-sites differences in assemblage composition (β3) for rare taxa accounted for 72% of the total taxonomic richness of rare taxa, while β3 for common taxa accounted for only 28% of the total taxonomic richness of common taxa (**Figure 6**).

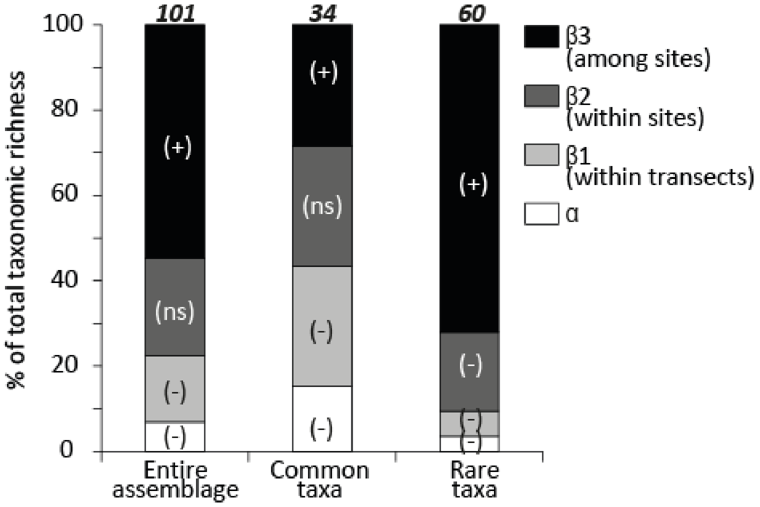

Figure 6 Relative contribution of additive diversity components to total taxonomic richness across three levels of spatial scales in the dry riverbed of the Albarine River, for the entire assemblage, the common taxa (> 0.3% of abundances) and the rare taxa (< 0.1% of abundances). Values are expressed as a percentage of total taxonomic richness (gamma diversity, in bold). The observed values were compared to expected values using individual-based randomizations (+ significantly larger, - significantly smaller, ns not significant).

DISCUSSION

Lateral organization of arthropod assemblages: riparian zones are the dominant source of dry riverbed colonists

The results of this study do not support the prediction that arthropod assemblages would differ among RZ-B, RZ-D and DRB. Rather, we found considerable overlaps in the composition of collected arthropod assemblages. Slight differences between DRB and RZ-D were mainly due to more frequent and more abundant taxa in riparian zones, while taxa that were specific to DRB were very scarce. The existence of such compositional overlap in spite of a much higher taxonomic richness in RZ-D compared to the DRB clearly support the conclusion that arthropod assemblages do not differ between RZ-D and DRB in the two studied rivers. A part of the observed compositional dissimilarity was necessarily due to nestedness resulting from differences in taxonomic richness, instead of taxa turnover (Baselga 2010). As a conclusion, DRB of these two temporary rivers are not habitats supporting unique species and display rather arthropod assemblages that are subsets of those from riparian zones.

Riparian assemblages were composed by a mix of taxa with strict habitat preferences for riparian habitats and generalist taxa able to colonize DRB. Habitat partitioning was particularly strong for detritivorous taxa, which were less represented in DRB compared to RZ-B and RZ-D. This result is rather surprising with regards to the large inputs of riparian organic matter that are generally reported in DRB, including in the Albarine River (Corti & Datry 2012). DRB are probably poor quality habitats for detritivorous species because sediment transport and deposition during flowing periods recurrently reset soil organic horizons. Because processes involved in mineral-organic complex are slow (Huang *et al.* 2005), DRB constitute slightly developed soils where the absence of humus probably limits the development of micro-organisms enticing detritivorous arthropods (Andersen and Nelson 2006). In addition, organic matter drying and photodegradation in sunlit DRB change leaf-litter chemistry and reduce its nutritive value for fungi and detritivorous arthropods (Austin & Vivanco 2006, Dieter *et al.* 2011). These findings contribute to a growing number of evidence demonstrating that temporary rivers functioned as punctuated biogeochemical reactors

(Larned *et al.* 2010, Corti *et al.* 2011, Datry *et al.* 2011). Micro-organisms and detritivorous arthropods decomposing organic matter during flowing periods are poorly active during dry periods, resulting in organic matter accumulation along dry riverbeds.

The strong overlap in the composition of RZ-B, RZ-D, and DRB assemblages indicates that riparian arthropods abundantly migrate towards DRB. This suggests that riparian zones and DRB are linked by a source-sink dynamic and density-dependence mechanisms favoring the rapid colonization of DRB by riparian arthropods (Leibold *et al.* 2004, De Meester & Bonte 2010). DRB constitute probably useful habitats where to survive, grow, and reproduce for many riparian taxa. As dry riverbeds are harsh environments with soil temperature sometimes exceeding lethal temperature of many organisms, movement of riparian arthropods may be diurnal and individuals may colonize DRB only at dusk, night and dawn when they are cool and humid places. DRB can supply food resources such as young shoots, micro-organisms, stranding aquatic invertebrates and preys and can favor foraging activities due to the absence of dense vegetation cover limiting the mobility of individuals. As a consequence, DRB could prevent species from competitive exclusion in riparian communities where they are bad competitors, by allowing immigration in habitats where they become good competitors (Hamilton & May 1977). By increasing individual fitness and changing interactions among population, DRB could alter the dynamic of riparian assemblages (den Doer 1990, Farnon Ellwood *et al.* 2009). In turn, high immigration rates could decrease temporarily competitive interactions in riparian zones and benefit to species with strict habitat preferences for riparian habitats. Ultimately, the benefit of the use of DRB by riparian communities strongly depends on arthropod abilities to resist to rewetting events, the latter eliminating species without inundation-resistant strategies and dispersing those who have them (Corti & Datry 2012). Arthropods that resist to rewetting events could generate a large input of arthropods in riparian zones. This input could cause the total number of individuals to grow beyond what riparian zones could support and provide a reserve of individuals available for re-colonization during following dry periods. Therefore, DRB and riparian zone are probably complementary and interrelated habitats driving riparian invertebrate biomass and diversity in temporary rivers.

Assemblage composition along longitudinal aquatic-terrestrial gradients

The prediction that assemblage would be structured longitudinally in dry riverbeds was not supported. Assemblage differences between sites distributed longitudinally over a 10 km distance were low, and the total taxonomic richness in DRB was mainly caused by within-site differences in assemblage composition. This result suggests that there is neither an elimination of water-sensitive species nor a growing complexity of assemblage structure with time since drying as we expected. In contrast, the composition of assemblages at sites that had dried recently was similar to that at sites that had dried four months ago. Flood events probably recurrently promote the downstream dispersal of terrestrial arthropods (Lambeets *et al.* 2010; Corti & Datry 2012), thereby homogenizing arthropod assemblages in riparian zones before they colonize DRB. In addition, the stochastic arrangement of microhabitats caused by flood disturbances, in both the riparian zone and DRB can be a strong driver of the segregation of taxa (Ward *et al.* 1999, Antvogel & Bonn 2001). The idea of an apparent stochasticity in the distribution of microhabitat and arthropods in DRB is supported by the fact that within-site diversity was not significantly different from the one expected by chance through individual-based randomizations. Terrestrial arthropods in DRB are thus mainly dependent to the structure and composition of arthropod assemblages in riparian zones and to the spatial arrangement of microhabitats in DRB. Consequently, operation that degrade habitat structure and quality of riparian zones such as wide-scale removal or non-regeneration of vegetation due to clearing and un-managed grazing and removal of sand and gravel bars (Lovett & Price 2007) will, in turn, alter arthropod assemblages in DRB. Riparian buffers extending over the entire river channel could be useful management practices in temporary rivers for conserving terrestrial arthropods (Marczak *et al.* 2010), and their efficiency may be increased by favoring a high diversity of microhabitats in both riparian and riverbed habitats.

In conclusion, our results indicate that lateral and longitudinal aquatic-terrestrial gradients have contrasted influence on the organization of aquatic and terrestrial arthropod assemblages in temporary rivers. Longitudinal aquatic-terrestrial gradients have been shown to have a strong influence on the composition of aquatic arthropod assemblages (e.g., Fritz & Dodds 2004, Arscott *et al.* 2010, Datry 2012, Datry *et al.* 2012). Rather, terrestrial arthropods assemblages are mainly structured laterally. As a consequence, colonization of riverbeds by aquatic and terrestrial arthropods and the organization of their assemblages could be mainly controlled by a lateral source-sink dynamic during flowing periods and a lateral source-sink dynamic during dry periods,

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Supplementary material S1 Total of individuals (Sum), percentage of occurrence (Occ) feeding guild and abbreviations of taxa collected exclusively at the Albarine River (AL), exclusively at the Asse River or at both rivers (B) according the sampling groups (1: in the riparian zone before the dry period, 2: in the riparian zone during the dry period, and 3: in the dry riverbed). PP: predator/polyphagous, Ph: phytophagous, D: detritivorous

Taxa		**Abbrev**	**Guild**	**River**	**Groups**	**Sum**	**Occ**
ARACHNIDA							
Araneae							
Agelenidae	*Malthonica nemorosa*	Malth.n	PP	AS	1.2.3	9	0,23
	Tegenaria agrestis	Tege.ag	PP	AS	1.2.3	7	0,20
	Tegenaria atrica	Tege.at	PP	AL	3	1	0,03
Atypidae	*Atypus affinis*	Atyp	PP	AL	2	1	0,03
Clubionidae	*Clubiona comta*	Club.c	PP	AL	1	4	0,12
	Clubiona genevensis	Club.g	PP	AS	2	1	0,03
	Clubiona lutescens	Club.l	PP	AL	3+1	4	0,12
	Clubiona terrestris	Club.t	PP	AL	1.2	5	0,12
Corinnidae	*Phrurolithus festivus*	Phrur.f	PP	AL	1.2.3	19	0,32
	Phrurolithus minimus	Phrur.m	PP	AL	1	2	0,06
Dysderidae	*Dysdera erythrina*	Dysd.e	PP	AL	1.2	17	0,37
Gnaphosidae	*Drassyllus lutetianus*	Drassy.l	PP	AS	1	1	0,03
	Drassyllus pumilus	Drassy.pu	PP	AS	1	2	0,03
	Gnaphosa dolosa	Gna.d	PP	AS	3+1	8	0,20
	Haplodrassus minor	Haplod.m	PP	AS	1	1	0,03
	Micaria pulicaria	Mica.pu	PP	AL	1	2	0,06
	Nomisia aussereri	Nomi	PP	AS	2	1	0,03
	Phaeocedus braccatus	Phaeo	PP	AS	1	1	0,03
	Trachyzelotes pedestris	Trachy	PP	AL	1	14	0,26
	Zelotes apricorum	Zel.ap	PP	AL	1	4	0,12
	Zelotes latreillei	Zel.la	PP	AL	1.2	2	0,06
	Zelotes tenuis	Zel.te	PP	AS	1	10	0,23
Linyphiidae	*Bathyphantes gracilis*	Bathy.g	PP	AL	3+1	3	0,09
	Bathyphantes nigrinus	Bathy.n	PP	AL	2	2	0,03
	Caviphantes saxetorum	cavi.s	PP	AL	3	2	0,03
	Centromerita bicolor	Centro.b	PP	AL	1	1	0,03
	Centromerus sylvaticus	Centro.sy	PP	AL	1.2	16	0,43
	Collinsia distincta	Colli.d	PP	AL	1	1	0,03
	Dicymbium tibiale	Dicy.t	PP	AL	1	2	0,06
	Diplocephalus cristatus	Dipl.c	PP	AL	1.2.3	29	0,63
	Diplocephalus picinus	Dipl.p	PP	AL	1	3	0,09
	Diplostyla concolor	diplos.c	PP	AL	1.2.3	162	1,90
	Gongylidium rufipes	Gon.r	PP	AL	3+1	3	0,09
	Janetschekia monodon	Janets	PP	AS	1.2	7	0,20
	Lessertinella kulczynskii	Lessert	PP	AL	1	1	0,03
	Macrargus rufus	Macrar	PP	AL	1	1	0,03
	Meioneta affinis	Meio	PP	AL	1	1	0,03
	Meioneta rurestris	Meio.r	PP	AL	3	4	0,09
	Mermessus trilobatus	Merm.t	PP	AL	2	2	0,06
	Micrargus herbigradus	Micra.h	PP	AL	1	1	0,03
	Microneta viaria	Micron	PP	AL	1.2	63	0,55
	Neriene clathrata	Nerie	PP	AL	1	2	0,06
	Oedothorax agrestis	Oedo.ag	PP	AL	3+1	23	0,23
	Oedothorax apicatus	Oedo.ap	PP	B	1.2.3	140	1,50
	Oedothorax retusus	Oedo.er	PP	AL	1.2.3	62	0,81
	Palliduphantes pallidus	Pallidu	PP	AL	1.2	8	0,23

Taxa		Abbrev	Guild	River	Groups	Sum	Occ
	Porrhomma microphtalmum	Porrh.n	PP	AS	1	2	0,06
	Prinerigone vagans	Prine	PP	AS	1	2	0,06
	Silometopus elegans	Silo.e	PP	AL	1	1	0,03
	Sintula corniger	Sint	PP	AL	1	2	0,06
	Syedra gracilis	Sye.g	PP	AL	1	1	0,03
	Tenuiphantes flavipes	Tenui.f	PP	AL	1.2.3	68	1,18
	Tenuiphantes tenuis	Tenui.te	PP	AL	1.2	12	0,35
	Troxochrus scabriculus	Troxoc	PP	AL	1.2	37	0,58
	Walckenaeria acuminata	Walc.ac	PP	AL	1	2	0,06
	Walckenaeria atrotibialis	Walct	PP	AL	1	2	0,06
	Walckenaeria nudipalpis	Walc.nu	PP	AL	1.2	9	0,23
	Walckenaeria vigilax	Walc.vi	PP	AL	3	2	0,06
Liocranidae	*Liocranoeca striata*	Liocr	PP	AL	1	4	0,12
	Scotina celans	Scot	PP	AL	2	15	0,06
Lycosidae	*Arctosa leopardus*	Arct.l	PP	AL	3	1	0,03
	Arctosa perita	Arct.p	PP	AS	1	2	0,03
	Arctosa similis	Arct.s	PP	AS	3+1	19	0,46
	Aulonia albimana	Aulo	PP	AL	1	5	0,06
	Pardosa agrestis	Pard.ag	PP	AL	3	1	0,03
	Pardosa agricola	Pard.agri	PP	AS	3+1	19	0,29
	Pardosa amentata	Pard.am	PP	AL	1	57	0,40
	Pardosa hortensis	Pard.hor	PP	B	3+1	53	0,89
	Pardosa morosa	Pard.mo	PP	B	3+1	4	0,12
	Pardosa prativaga	Pard.pra	PP	AL	1	7	0,20
	Pardosa proxima	Pard.pro	PP	B	3+1	24	0,29
	Pardosa pullata	Pard.pul	PP	AL	1	1	0,03
	Pardosa saltans	Pard.sa	PP	AL	3+1	82	1,15
	Pardosa wagleri	Pard.wa	PP	B	1.2.3	188	1,90
	Piratula hygrophila	Pira.hy	PP	AL	3+1	37	0,46
	Piratula latitans	Pira.la	PP	B	1	3	0,09
	Trochosa ruricola	Troch.ru	PP	AL	3+1	48	0,72
	Trochosa terricola	Troch.ter	PP	AL	1.2	82	0,98
	Xerolycosa miniata	Xero.m	PP	AS	1	1	0,03
Mimetidae	*Ero furcata*	Ero.f	PP	AL	2	2	0,06
Philodromidae	*Thanatus vulgaris*	Thana	PP	AS	1	2	0,06
Pisauridae	*Pisaura mirabilis*	Pis.m	PP	AL	1	2	0,06
Salticidae	*Icius subinermis*	Icius	PP	AS	1	1	0,03
	Myrmarachne formicaria	Myrma	PP	AL	1	1	0,03
	Neon reticulatus	Neon	PP	AL	1	2	0,06
	Saitis barbipes	Saiti	PP	AS	1	7	0,20
	Sitticus distinguendus	Sitti.d	PP	AS	1.2.3	15	0,32
Tetragnathidae	*Pachygnatha degeeri*	Pachy.d	PP	AL	1	4	0,03
Theridiidae	*Euophrys frontalis*	Euo.f	PP	AL	1.2	2	0,06
	Euryopis flavomaculata	Eur.f	PP	AL	1	8	0,20
	Robertus arundineti	Rob.a	PP	AS	1	1	0,03
	Robertus lividus	Rob.l	PP	AL	1.2.3	5	0,12
	Robertus neglectus	Rob.n	PP	AL	1	1	0,03
Thomisidae	*Ozyptila praticola*	Ozy.pr	PP	AL	1.2	11	0,23
Titanoecidae	*Nurscia albomaculata*	Nursc	PP	AS	1	2	0,06
	Zodarion italicum	Zod.it	PP	AL	1.2	52	0,58
Zodariidae	*Zora spinimana*	Zora.sp	PP	AL	1	6	0,17
Opiliones		Opi	PP	B	1.2.3	212	2,85
Pseudoscorpionida		Pseu	PP	AL	1.2	96	1,67
CHILOPODA		Chilo	PP	AL	1.2.3	49	1,12

Taxa		Abbrev	Guild	River	Groups	Sum	Occ
DIPLOPODA		Diplo	D	AL	1.2.3	197	1,67
Iulidae		Iul	Ph	AL	1.2	71	1,04
DIPLURA		Diplu	PP	AL	1	2	0,03
INSECTA							
Archaeognatha		Archa	Ph	AL	1.2	25	0,40
Blattoptera		Blatt	PP	AL	2	2	0,06
Coleoptera							
Anobiidae		Ano	Ph	AL	2	1	0,03
	Anobium hederae	Ano.h	Ph	AL	2	1	0,03
Anthicidae	Anthicidae	Anth	PP	AS	3+1	6	0,14
	Anthicus antherinus	Anthnt	PP	AL	3+1	16	0,12
	Anthicus sp.1	Anth1	PP	AS	2	1	0,03
	Anthicus sp.2	Anth2	PP	AS	2	1	0,03
	Endomia occipitalis	Endo.o	PP	AL	1.2.3	19	0,37
	Endomia sp.1	Endo1	PP	AS	1.2	2	0,06
	Notoxus sp.	Noto	PP	AS	1	1	0,03
	Stricticollis sp.	Strict	PP	AS	1.2.3	5	0,14
Aphodiidae	*Melinopterus sp.1*	Meli	D	AL	1	2	0,06
Buprestidae	*Trachys fragariae*	Trachys.f	Ph	AL	2	1	0,03
	Trechus obtusus	Tre.o	Ph	AL	1	3	0,09
Byrrhidae	Byrrhidae sp.1	Byrr	Ph	AL	1	4	0,09
	Porcinolus murinus	Por.m	Ph	AL	2	1	0,03
Carabidae	*Agonum spp.*	Ago	PP	AL	1.2.3	12	0,20
	Amara eurynota	Amar	Ph	AL	3+1	13	0,29
	Anchomenus dorsalis	Ancho	PP	AL	1.2.3	70	0,52
	Anthracus consputus	Anthra	PP	AL	1.2.3	46	0,86
	Asaphidion spp.	Asaph	PP	B	1.2	5	0,14
	Badister bullatus	Badis	PP	AL	1.2	6	0,17
	Bembidion concoeruleum	Bemb.con	PP	AS	3+1	2	0,06
	Bembidion quadrimuculatum	Bemb.q	PP	AL	1.2	4	0,06
	Blemus discus	Blem.d	PP	AL	2	1	0,03
	Carabidae sp.1	Cara1	PP	AL	1	17	0,20
	Carabidae sp.2	Cara2	PP	AL	1	14	0,17
	Carabidae sp.3	Cara3	PP	AL	1	3	0,09
	Carabus auratus	Carau	PP	AL	1	14	0,23
	Carabus coriaceus	Cara.cor	PP	B	1.2.3	15	0,40
	Carabus nemoralis	Cara.n	PP	AL	1	2	0,06
	Chlaeniellus vestitus	Chlae	NA	AL	3	1	0,03
	Clivina collaris	Cliv.c	PP	AL	1	5	0,09
	Leistus fulvibarbis	Leis.f	PP	AL	3+2	2	0,06
	Lophyra flexuosa	Loph.f	PP	AS	1	1	0,03
	Metallina lampros	Metal.l	PP	AL	3+2	5	0,09
	Nebria brevicollis	Neb.b	PP	AL	3+2	17	0,09
	Notiophilus sp.	Notio	PP	AL	1	2	0,06
	Ocydromus atrocoeruleus	Ocyd	PP	AL	3+1	3	0,09
	Ocydromus decorus	Ocyd.d	PP	AL	3+2	15	0,23
	Ocydromus femoratus	Ocyd.f	PP	AL	1.2	23	0,26
	Ocydromus testaceus	Ocyd.tes	PP	B	1.2.3	21	0,37
	Ocydromus tetragrammus	Ocyd.t	PP	AL	1.2.3	41	0,35
	Oodes helopioides	Ood.h	PP	AL	3	1	0,03
	Ophonus sp.1	Opho1	Ph	AL	3+2	3	0,06
	Oxypselaphus obscurus	Oxy.o	PP	AL	2	2	0,03
	Panagaeus sp.1	Pana1	PP	AL	1	1	0,03
	Paranchus albipes	Paran	PP	AL	1.2.3	43	0,58

Taxa		Abbrev	Guild	River	Groups	Sum	Occ
	Perileptus areolatus	Peri.a	PP	AL	3	1	0,03
	Platynus assimilis	Platy	PP	AL	1	1	0,03
	Poecilus spp.	Poe	PP	B	3+1	16	0,26
	Pterostichus cristatus	Pte.c	PP	AL	2	1	0,03
	Pterostichus madidus	Pte.ma	PP	AL	3+2	5	0,14
	Pterostichus melanarius	Pte.me	PP	AL	3+1	5	0,12
	Pterostichus niger	Pte.n	PP	AS	3+2	3	0,09
	Pterostichus sp.1	Pte1	PP	AL	1.2	5	0,14
	Pterostichus vernalis	Pte.v	PP	AL	1.2.3	9	0,14
	Scarites terricola	Sca.t	PP	AS	1.2	46	0,63
	Stomis pumicatus	Sto.p	PP	AL	1.2	5	0,12
	Syntomus obscuroguttatus	Synt.o	PP	AL	2	1	0,03
	Tachys bistriatus	Tac.b	PP	AL	3+1	5	0,14
	Tachyura spp.	Tachyu	PP	B	1.2	2	0,06
	Trechus quadristriatus	Tre.q	PP	AL	1.2.3	30	0,52
Cerambycidae	*Grammoptera ruficornis*	Gram.r	Ph	AL	1	1	0,03
Chrysomelidae	*Chaetocnema sp.*	Chaet	Ph	AL	3+1	50	0,55
	Chrysomelidae sp.1	Chryso1	Ph	AL	1	2	0,06
	Chrysomelidae sp.2	Chryso2	Ph	AL	3	1	0,03
	Crepidodera sp.	Crepi	Ph	AL	1.2	7	0,12
	Longitarsus spp.	Long	Ph	AL	1.2.3	10	0,26
	Oomorphus concolor	Oom.c	Ph	AL	1.2	12	0,32
	Pachnephorus tessellatus	Pachn.t	Ph	AS	1.2	22	0,14
	Phyllotreta spp.	Phy	Ph	B	1.2.3	69	0,95
	Psylliodes attenuatus	Psy	Ph	AL	3	2	0,06
	Pyrrhalta viburni	Pyrr.v	Ph	AL	1	1	0,03
Ciidae		Ciid	Ph	AL	1.2	2	0,06
Clambidae	*Clambus sp.*	Clamb	D	AL	1.2.3	21	0,40
Coccinellidae	*Tytthaspis sedecimpunctata*	Tytth.s	Ph	AL	2	1	0,03
	Vibidia duodecimguttata	Vibi	Ph	AL	2	1	0,03
Corylophidae		Cory	Ph	AS	2	1	0,03
	Sericoderus lateralis	Seric.l	Ph	AL	1.2	3	0,09
Cryptophagidae	*Atomaria sp.*	Ato	Ph	AL	1.2.3	111	1,38
	Caenoscelis sp.	Caenos	Ph	AL	1	11	0,14
	Cryptophagus sp.	Crypt	Ph	AL	1.2	39	0,63
Curculionidae	*Acalles spp.*	Acall	Ph	AL	1.2	9	0,26
	Adexius scrobipennis	Adex.s	Ph	AL	2	1	0,03
	Archarius sp.1	Archa1	Ph	AL	1	10	0,20
	Aulacobaris coerulescens	Aulaco.c	Ph	AL	1	1	0,03
	Barypeithes pellicidus	Baryp	Ph	AL	1.2.3	55	0,66
	Brachysomus hirtus	Brachy.h	Ph	AL	1	1	0,03
	Donus sp.	Don	Ph	AL	1	2	0,06
	Dorytomus	Dory	Ph	AL	1	1	0,03
	Hemitrichapion reflexum	Hemit.ref	Ph	AL	3+1	2	0,06
	Otiorhynchus rugosostriatus	Otio.r	Ph	AL	1.2	2	0,06
	Otiorhynchus sp.	Otio1	Ph	AS	1	1	0,03
	Polydrusus sericeus	Polyd.s	Ph	AL	2	1	0,03
	Polydrusus sp.1	Polyd1	Ph	AS	1	1	0,03
	Cotaster uncipes	Cata.u	Ph	AL	1.2	2	0,06
	Curculionidae sp.1	Cucu1	Ph	AL	1	1	0,03
Dasytidae	*Dasytes sp.*	Dasy	Ph	AL	3	1	0,03
Drilidae	*Drilus flavescens*	Dril.f	PP	AL	1	1	0,03
Dryopidae	*Esolus sp.*	Eso	D	AL	1.2.3	7	0,14
	Limnius volckmari	Limn.v	D	AL	3	1	0,03

Taxa		**Abbrev**	**Guild**	**River**	**Groups**	**Sum**	**Occ**
	Pomatinus substriatus	Poma.s	D	AL	2	2	0,06
Dynastinae	*Bothynus sp.*	Bothy	D	AL	3+2	4	0,09
Elateridae		Ela	Ph	AS	1	2	0,06
	Adrastus sp.	Adras	Ph	AS	2	1	0,03
	Agriotes sp	Agrio	Ph	AL	1	2	0,06
	Melanotus sp.	Mela	Ph	AS	2	1	0,03
	Zorochros sp.1	Zoro1	Ph	AS	1.2.3	7	0,20
	Zorochros dermestoides	Zoro.d	Ph	AL	1.2.3	173	1,18
Haliplidae	*Haliplus lineatocollis*	Halip.l	Ph	AL	3	1	0,03
Hydrophilidae	*Cercyon sp.*	Cercy	D	AL	1.2.3	11	0,29
	Georissus crenulatus	Geori.c	PP	AL	1.2	12	0,17
Lampyridae		Lamp	PP	AL	2	7	0,20
Latridiidae	*Corticaria spp.*	Corti2	Ph	AL	1.2	6	0,14
	Corticarina spp.	Corti1	Ph	AL	1.2.3	14	0,29
Leiodidae	*Catops fuliginosus*	Catops.f	D	AL	1.2.3	11	0,26
	Colenis immunda	Colen.i	D	AL	1	2	0,06
	Leiodes polita	Leio.p	D	AL	1	3	0,09
	Nargus spp.	Narg	D	AL	1.2.3	71	0,63
	Ptomaphagus sp.	Ptom	D	AL	1.2	22	0,40
	Sciodrepoides watsoni	Scio.w	D	AL	1.2	16	0,23
Limnichidae	*Pelochares versicolor*	Pelo.v	D	AS	1.2.3	12	0,26
Lucanidae	*Dorcus parallelipipedus*	Dorc.p	D	AS	2	1	0,03
	Lucanus cervus	Luca.s	D	AL	3	1	0,03
Pselaphidae		Psela1	PP	AS	1	1	0,03
	Pselaphinae spp.	Psela2	PP	AL	1.2.3	132	1,24
	Pselaphus heisei	Psela.h	PP	AL	3	1	0,03
Scarabaeidae	*Hoplia hungarica*	Hop.h	PP	AS	1	3	0,03
	Psammodius sp.	Psam	D	AS	1	8	0,09
	Rhyssemus.germanus	Rhys.g	D	AS	1	1	0,03
Scydmaenidae	*Stenichnus collaris*	Ste.c	PP	AL	1.2	3	0,09
	Phosphuga atrata	Phos	PP	AL	1.2	6	0,14
Silphidae		Silph	D	AL	2	1	0,03
Staphylinidae	Aleocharinae	Aleo	NA	B	1.2.3	519	3,77
	Ancyrophorus flexuosus	Ancyr.f	D	AL	1	24	0,17
	Anthobium atrocephalum	Anthob	NA	AL	1.2	4	0,12
	Astenus sp.	Ast	NA	AL	2	1	0,03
	Deleaster dichrous	Delea.d	NA	AL	3+1	2	0,06
	Micropeplus sp.1	Microp	D	AL	2	1	0,03
	Mycetoporus spp.	Myce	Ph	AL	1.2	7	0,17
	Omalium spp.	Oma	NA	AL	1.2.3	12	0,32
	Oxytelinae	Oxyt	D	AL	1.2.3	48	0,89
	Paedericus spp.	Paed1	PP	AL	3+1	8	0,14
	Paederinae spp.	Paed2	PP	AL	2	2	0,06
	Paederus spp.	Paed	PP	B	1.2.3	20	0,52
	Proteinus spp.	Prot	PP	AL	1	4	0,09
	Staphylininae spp.	Staphn	D	AL	1.2.3	61	1,18
	Stenus spp.	Ste	PP	B	1.2.3	52	1,18
	Tachyporinae spp.	Tach	Ph	AL	1.2	16	0,40
	Xantholinae spp.	Xanth	PP	B	1.2.3	12	0,29
Tenebrionidae		Tene	D	AS	1	1	0,03
Throscidae		Thros	D	AS	1	3	0,03
Dermaptera		Derm	PP	AL	1.2	7	0,12
	Labidura riparia	Labi.r	PP	AS	1.2.3	494	3,19
Hemiptera		Hemi.A	PP	B	1.2.3	21	0,46

Taxa		**Abbrev**	**Guild**	**River**	**Groups**	**Sum**	**Occ**
Aphidoidea		Aphid	Ph	B	1.2.3	180	1,84
Cicadellidae		Cica	Ph	B	1.2.3	34	0,58
Heteroptera		Hete	PP	B	1.2.3	97	1,61
Hymenoptera							
Formicidae	*Aphaenogaster subterranea*	Aphaen	PP	B	1.2.3	58	0,75
	Camponotus aethiops	Camp	PP	AS	1	1	0,03
	Camponotus vagus	Camp.v	PP	AS	3+2	2	0,06
	Cardiocondyla elegans	Cardio.e	PP	AS	1.2.3	54	0,52
	Chthonolasius sp.	Chton	PP	AL	2	1	0,03
	Formica fusca	Form.f	PP	AL	3	1	0,03
	Formica gagates	Form.g	PP	AL	1	1	0,03
	Formica selysi	Form.s	PP	AS	1.2.3	137	1,09
	Lasius alienus	Las.al	PP	AL	3	1	0,03
	Lasius brunneus	Las.br	PP	AL	1.2.3	16	0,26
	Lasius emarginatus	Las.em	PP	AL	1.2.3	280	1,01
	Lasius flavus	Las.fl	PP	AL	1	1	0,03
	Lasius fuliginosus	Las.fu	PP	AL	1.2.3	479	0,58
	Lasius neglectus	Las.ne	PP	AS	1	3	0,06
	Lasius niger	Las.ni	PP	AL	1.2.3	582	1,96
	Lasius paralienus	Las pa	PP	AL	1.2	3	0,06
	Lasius platythorax	Las.pl	PP	AL	1.2.3	39	0,55
	Lasius sp.1	las1	PP	AL	1	3	0,09
	Myrmecina graminicola	Myrme.g	PP	AL	1.2	104	1,52
	Myrmica rubra	Myrm.rub	PP	AL	1.2.3	521	2,59
	Myrmica ruginodis	Myrm.rug	PP	AL	1.2	16	0,32
	Myrmica sp.1	Myrm1	PP	AL	1	1	0,03
	Pheidole pallidula	Pheid.p	PP	AS	1.2.3	79	0,55
	Plagiolepis spp.	Plagi	PP	B	3+2	6	0,12
	Ponera sp.	Pon	PP	AL	2	1	0,03
	stenamma debile	stena	NA	AL	1.2	4	0,09
	Tapinoma sp.	Tapi	PP	B	3+1	2	0,06
	Temnothorax sp.	Temn	PP	B	1.2.3	177	1,61
	tetramorium sp.	tetra	PP	AL	2	7	0,06
Orthoptera		Orth	D	B	1.2.3	55	1,21
Gryllidae		Gryll	PP	AL	3	2	0,03
Siphonaptera		Siph	Parasites	AL	1.2.3	63	1,06
MALACOSTRACA							
Oniscidea		Onis	D	B	1.2.3	2071	5,01

5

EFFETS DES ASSECHEMENTS SUR LES COMMUNAUTES D'INVERTEBRES RIPARIENS

Article 3

Effects of river drying on riparian arthropod communities in a French temporary river (Albarine, France)

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En préparation

ABSTRACT

Aquatic and terrestrial ecosystems are intimately linked. Although river water and aquatic prey subsidies are important drivers of adjacent riparian communities, the effects of river drying on riparian arthropods remain poorly understood. In this study, we collected riparian arthropods at three perennial sites and at four temporary sites before and during a summer dry period. We first predicted mean taxonomic richness and abundance of terrestrial arthropods to be lowest in temporary sites, and assemblage composition to change during the dry period owing to cascading effects of river drying on predators and hygrophilous taxa. Second, we predicted temporal variations of community composition and cumulative taxonomic richness to be highest at temporary sites, owing to a higher variability in environmental conditions caused by drying and rewetting cycles. River drying had no detectable effects on the taxonomic richness and abundance of riparian arthropods and on sediment moisture content, since we found similar decreasing temporal patterns for these three variables at perennial and temporary sites. Community composition in temporary and perennial sites differed only during the dry period, suggesting dispersal occurred during the flowing period. Although compositional variability over time at temporary sites was not higher than at perennial sites, temporary sites showed highest cumulative taxonomic richness. Our results indicate that rivers running dry can support rich riparian communities and support the view of temporary rivers as dynamic ecosystems contributing to regional biodiversity.

Key-words: intermittent river, ground-dwelling arthropods, aquatic-terrestrial linkages, cascade effect, hygrophilic, predator

INTRODUCTION

Ecosystem dynamics is rarely confined to a particular habitat and energy transfer across ecosystem boundaries affects population, community and food-web dynamics (Polis *et al.* 1997). Riparian zones are dynamic ecosystems that link terrestrial and aquatic habitats (Naiman & Décamps 1997, Ward *et al.* 1999, Wiens 2002). Reciprocal flows of energy and nutrients promote the biodiversity and the productivity of riparian and river ecosystems (Nakano *et al.* 1999, Baxter *et al.* 2005). Notably, water, emerging insects, and organic matter from aquatic ecosystems are drivers of consumer populations in riparian zones which can in turn alter community and food web dynamics (Polis *et al.* 1997, Ballinger & Lake 2006, Akamatsu & Toda 2011).

River flow fluctuations influence the composition and distribution of terrestrial communities in riparian zones (Junk *et al.* 1989, Bonn *et al.* 2002). Fluvial processes occurring during floods result in repeated channel movements that create a patchwork of habitats in which communities are structured (Ward *et al.* 1999, Wiens 2002). Floods control community composition through the selection and dispersion of inundation-resistant taxa (Bates *et al.* 2007, Lambeets *et al.* 2008) and by influencing the abiotic factors of habitats such as sediment grainsize and moisture (Ballinger *et al.* 2007). In temporary rivers, streambed drying events influence abiotic factors and shape riparian communities at various temporal and spatial scales (Katz *et al.* 2011). Nevertheless, in contrast to flooding, the effects of river drying on riparian communities have been largely overlooked.

River drying can have cascading effects on riparian communities, including plants, arthropods and bats (Stromberg *et al.* 2009, Hagen & Sabo 2012, Katz *et al.* 2012, McCluney & Sabo 2012). The terrestrial fauna inhabiting riparian zones consists mainly in predator arthropod species (Rykken *et al.* 2007, Horn *et al.* 2009, Lambeets *et al.* 2008) that are strongly dependent to aquatic insect prey (Hering & Plachter 1997, Paetzold *et al.* 2005). Additionally, numerous riparian arthropods show narrow niche breadth with strong habitat preferences for humid and moist habitats (i.e. hygrophilic species) (Andersen 1985, Lambeets *et al.* 2008). Therefore, declines in aquatic insect prey and in sediment moisture should have strong negative effects on riparian arthropod communities. However, the response of riparian communities to river drying could vary according to the ability of species to shift their diet regime toward terrestrial resources (Hering & Plachter 1997, Sanzone *et al.* 2003, Greenwood & McIntosh 2010) and to tolerate dry conditions (Andersen 1985).

Understanding temporal variability in species composition is a central aspect of community ecology, because it determines the total number of species that a habitat can support over time (Magurran *et al.* 2010). In particular, variations in environmental conditions can generate temporal variability in species composition and high cumulative taxonomic richness by controlling emigration and immigration rates of species within a regional species pool (Gaston 2000, Mouquet *et al.* 2002). In rivers, repeated drying and rewetting cycles cause high variation in environmental conditions including sediment moisture, temperature and vegetation cover (Steward *et al.* 2011, Katz *et al.* 2012, Datry *et al.* 2012), which in turn could change community composition over time. Indeed, many riparian arthropods display biological traits, such as the ability to fly and to drift in river flow that enable them to respond quickly to spatial and temporal environmental changes (Desender 1989, Bates *et al.* 2007). In addition, case studies in temporary rivers have reported high temporal variability in plant species richness and community structure over time (Stromberg *et al.* 2009, Katz *et al.* 2012), two factors that strongly influence the composition of arthropod communities (Schaffers *et al.* 2008). Consequently, temporal variations in environmental conditions are likely to be higher in temporary than in perennial sections of rivers. In turn, this could influence temporal variability of community composition and increase cumulative taxonomic richness.

In this study, we addressed the effects of river drying on taxonomic richness, abundance and composition of riparian arthropod communities in the Albarine River, France. We collected riparian arthropods using pitfall traps at three perennial sites and at four temporary sites before and during a summer dry period. We predicted that 1) mean taxonomic richness and abundance of terrestrial arthropods would be lowest at temporary sites during the dry period owing to cascading effects of river drying on predators and hygrophilous taxa, 2) differences in composition of arthropod communities between temporary and perennial sites would be higher during the dry periods than the flowing periods, owing to the dispersal of riparian arthropods during the flowing period and 3) temporal variability of community composition and cumulative taxonomic richness would be highest at temporary sites, owing to a higher variation in environmental conditions (*e.g.* vegetation structure and sediment moisture) caused by repeated drying and rewetting cycles.

METHOD

Study sites

The study was conducted in 2010 in the Albarine River, an alluvial, gravel-bed temporary river in France. The Albarine River drains a 313 km^2 catchment in eastern France (**Figure 1**) and has a mean annual discharge of 6.88 m^3.s^{-1} (Datry *et al.* 2011). The regional climate is temperate and broadly characterized by wet winters and warm, dry summers. Average annual precipitation range from 1000 to 1200 mm per year. The downstream section of the Albarine River flows across an alluvial plain before joining the Ain River (**Figure 1**). Along this alluvial plain, the flow regime is temporary and drying occurs seasonally due to seepage into the underlying aquifer (Datry *et al.* 2011). River drying starts at the confluence with the Ain River during low runoff period and gradually extends upstream over a 10 km-long temporary section, up to which the flow regime is perennial. Long dry periods of 4 to 5 months leading to a completely dry river bed occur each year in summer until autumn (Datry *et al.* 2011).

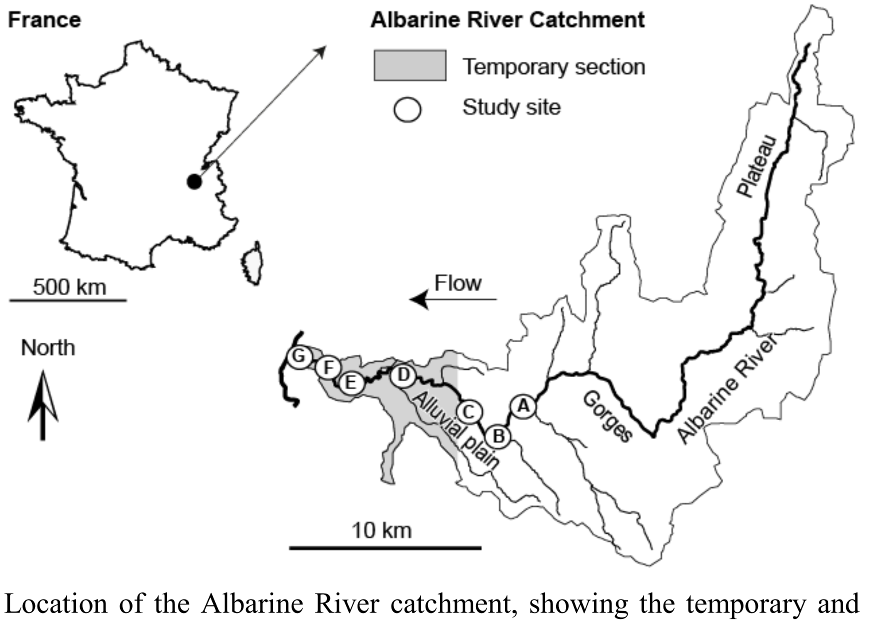

Figure 1 Location of the Albarine River catchment, showing the temporary and perennial sections and the seven study sites

Seven sites along the Albarine River (from A to G) were sampled for terrestrial arthropods, including three sites in the perennial section and four sites in the temporary section (**Figure 1)**. Sites were scattered 2 to 4-km apart. Length of each site was 10x the mean width of the active channel to encompass several distinct habitat types (*e.g.* gravel and sand bars, forested habitats) (Corti *et al.* in revision). We defined the active channel as the area constituted of inundated and exposed bed sediments between established edges of perennial, terrestrial vegetation and abrupt changes in slope (Gregory *et al.* 1991). The width of the active channel was 18m on average. The active channel at the Albarine River was bordered by a riparian forest dominated by *Populus sp*., *Alnus glutinosa* and *Fraxinus excelsior* trees. At temporary sites, mean annual flow permanence (defined as the percentage of the year that a site is flowing) calculated for the last 25 years varies between 80% at site D and 55% at site G (Datry *et al.* 2011a).

Sampling design

Sites were sampled for terrestrial arthropods using pitfall traps (Spence & Niemela 1994, Corti *et al. in revision*). Sites were sampled four times at two month intervals during two hydrological periods; twice before all the sites dried (April and June 2010) and twice while temporary sites were dry (August and October 2010). During the dry period, once a site dried, it stayed dry with no partial reestablishment of flow between sampling dates.

Pitfall traps were installed along transects crossing the active channel perpendicularly to flow direction (**Figure 2**). We defined three transects offset from each other by 35 to 45m at each site, depending on site length. Transect length was 2x the width of the wetted river bed measured at base flow condition. The average width of the wetted river bed was of 15m at the Albarine. Before the dry period, we installed four pitfall traps scattered at least three meters apart on both sides of the river bed at each transect: two at the edges of the transect and two 0.2 - 0.5m from the waterline (**Figure 2**). Position of pitfall traps never changed over the full period of the study. Pitfall traps consisted of 7-cm tall, 8-cm diameter plastic containers inserted in sediments until flush with the river bed surface. Ethylene glycol (15 ml) was added to each container as a preservative, and the containers were covered with a 15-cm diameter plastic plate to keep rain out. All pitfall traps were deployed for 7 days after which the contents were transferred to plastic bags and stored until analysis. The ethylene glycol served as a sample preservative.

Our sampling design theoretically comprised a total of 336 samples (7 sites × 3 transects × 4 samples per transect × 4 sampling dates). However, a total of 6 pitfall samples (1.5 %) were lost due to disturbance by digging mammals (*e.g.* Wild boar), small rain events, rising groundwater or improper handling.

In addition, one 1-L sediment sample was collected at each transect at equal distance of two pitfall traps, transferred to a sealable plastic bag and sealed for the determination of sediment moisture content.

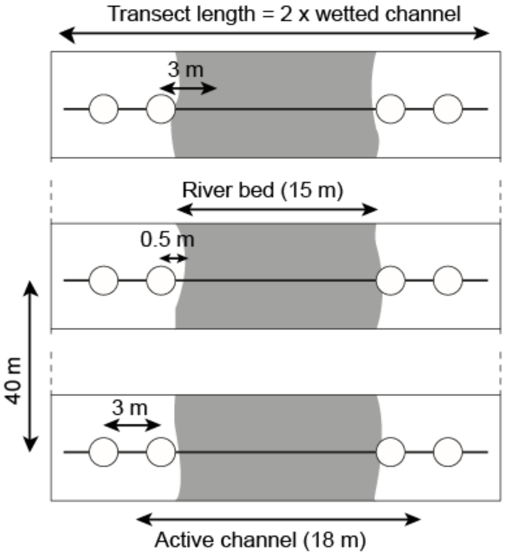

Figure 2 Location of the pitfall traps along transects. Pitfall traps (white circles) were scattered at least 3-m apart on both side of the river bed at each transect

Laboratory procedures

Arthropods from pitfall traps were rinsed with tap water above a 63-µm mesh sieve and the retained material was preserved in 70% ethanol. We identified arthropods from pitfall-trap samples to the lowest practical taxonomic level - species or genus for most Coleoptera, Aranea, and Formicidae, and family, class, or order for other taxa. Species identifications were made by the authors and numerous collaborators (see section 'Acknowledgments'), using published keys (*e.g.* Gaetan du Chatenet 2005) and reference collections. Species were named according to the nomenclature of the Fauna Europaea Web Service (2012). Collembola, Acarina, and aerial taxa (*e.g.* Diptera, Apidae, and Lepidoptera) were not included in data analyses as pitfall traps are not an appropriate sampling method for these taxa (Yi *et al.* 2012, Corti *et al. in revision*). Immature spiders and larvae were also removed from the dataset as accurate identifications were not possible. Overall, 42% of individuals were determined to species level, 18% to genus or sub-family level and 40% to family, order or class

To determine the moisture content of sediment samples, two randomly-selected subsamples of c. 50 mL from each 1-L sample were weighed wet, dried at 60 °C to constant mass and reweighed. Moisture content was calculated from differences between wet and dry mass.

Biological traits

Arthropods were assigned to feeding guilds and Araneae, Carabidae and Formicidae species were characterized according to their moisture and shading preferences. Designation to feeding guilds (predator/polyphagous, phytophagous or detritivorous) was derived from existing literature (*e.g.* Hering & Plachter 1997; Rykken *et al.* 2007) and general knowledge. The predator/polyphagous guild included species which opportunistically consume organic matter, live prey or carrions. Araneae, Carabidae and Formicidae were assigned to moisture and shading ecotypes on the bases of general knowledge reported in the relevant literature (*e.g.* Bonn *et al.* 2002, Entling *et al.* 2007, Lambeets *et al.* 2008) or following consultation with taxonomists (see section 'Acknowledgements'). Based on these ecotypes, we defined 3 ecological groups: 1) xerophiles, for species occurring in arid or warm conditions and mainly restricted to scarcely vegetated habitats, 2) hygrophiles, for species occurring in moist and humid habitats with more dense vegetation cover and 3) eurytopic, for ubiquitous species occurring in a wide range of habitats taxa or associated with habitats neither too arid nor too humid.

Data analysis

Effect of river drying on community structure and composition

We used a generalized linear modeling (glm) to test the effects of flow regime (temporary versus perennial), hydrological periods (before versus during the dry period) and their interactions on the following variables: i. taxonomic richness and abundance of the whole community, ii. taxonomic richness and abundance of predator, xerophilic and hygrophilic arthropods and iii. taxonomic richness and abundance of taxa common to temporary and perennial sites. Glm were ran assuming a quasi-poisson distribution for the taxonomic richness and log-transformed abundance data, since these data sets often exhibit over-dispersion and can contained a large number of zeros (Potts & Elith, 2006). Values were summed by transect, averaged by sites and then averaged by hydrological period, as we were interested in arthropod responses to river drying, rather than in seasonal or between-site variations.

We used the Bray-Curtis dissimilarity index to compare arthropod community composition between perennial and temporary sites during each hydrological period. Patterns of dissimilarity were analyzed using non-metric multidimensional scaling (NMDS). A permutational multivariate analysis of variance called ADONIS (Anderson 2001) was used to test for differences in community composition between flow regimes during each hydrological period. ADONIS returns a statistic R^2, which is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation), and a *p*-value estimated by repeated permutations of the data (Anderson 2001). Values were summed by transect, and then averaged by sites to considered between-date variability in assemblage composition. NMDS and the ADONIS analysis were ran with arthropod abundance data, after removal of taxa that comprised < 0.1 % of individuals, to minimize the influence of rare or inadequately sampled taxa. Data were square-root-transformed and double-standardized (Wisconsin method), by standardizing taxa by their maxima, and then standardizing samples by sample totals (Oksanen *et al.* 2012).

Procrustes analyses were performed to compare how differences in community composition between flow regimes differed for the two hydrological periods. Procrustes rotation uses uniform scaling (expansion and contraction) and rotation to minimize the squared differences between two ordinations (Oksanen *et al.* 2012). As a result, the ordinations of sites before and during the dry period are shown simultaneously, and for each site, arrows of varying lengths joined their respective positions in the two ordinations. For this analysis, values were first summed by transect, averaged by sites and then averaged by hydrological period for final sample size of 3 perennial sites and 4 perennial sites for each of the two hydrological periods. Finally, we assessed changes in relative abundance and occurrence of taxa between the two hydrological periods in temporary sites and in perennial sites by conducting an Indicator Species analysis (INDVAL) (Dufrêne & Legendre 1997). INDVAL calculates an indicator value for each taxon by combining information about species relative abundance and relative frequency of occurrence. An indicator value of 100% indicates that all individuals of a taxon were found exclusively in a group, and that this taxon was collected in all samples from that group. Indicator values were tested for statistical significance using Monte-Carlo procedures (1000 permutations).

Temporal variability of community composition and cumulative taxonomic richness

We used the multivariate dispersion analysis (Anderson *et al.* 2006) to assess whether compositional variability of arthropod communities over the full period of the study (i.e. temporal turnover) was higher in temporary sites compared to perennial sites. Multivariate dispersion analysis for a group of samples calculates the average distance of group members to the group centroid in a multivariate space. This analysis was performed using Bray-Curtis dissimilarity measures calculated from presence/absence data summed by transect and then averaged by site. We used a permutation test to assess the significance of differences in dispersion between temporary and perennial sites.

The rarefaction method (*sensu* Gotelli & Colwell 2001) was used to compare cumulative taxonomic richness between temporary and perennial sites over the full period of the study. Rarefaction standardizes the sampling effort through random sub-sampling of a dataset and provides the expected taxonomic richness in a given number of samples (Gotelli and Colwell 2001).

All statistical analyses were carried out using R software (R Development Core Team 2012) and functions in the package Stats (R Development Core Team 2012), Vegan (Oksanen *et al.* 2012) and Labdsv (Roberts 2012). For rarefaction curves, differences among sampling groups were considered statistically significant if CIs did not overlap. For other statistical analysis, $p < 0.05$ was used to indicate statistical significance.

RESULTS

More than 12,100 riparian arthropods belonging to 256 taxa were collected in the Albarine River (**Supplementary material S1**). The 5 most frequent and abundant taxa were Oniscidea (Crustacea, 7.1% of occurrences), Aleocharinae (Coleoptera, 5.3%), Opiliones (3.9%) *Myrmecina graminicola* (Latreille 1802, Formicidae, 3.0%), and *Temnothorax sp.* (Formicidae, 3.0%). Sixty taxa (23%) were collected in only one sample.

Effect of river drying on community structure

Taxonomic richness of all arthropods, of predator and hygrophilic arthropods and of arthropods common to temporary and perennial sites was higher at temporary sites (**Table 1, Figure 3**). Taxonomic richness of xerophilic arthropods did not differ between flow regimes or hydrological periods. Taxonomic richness of eurytopic arthropods did not differ between flow regimes, but were higher during flowing periods. In addition, the abundance of all arthropods, of predator, xerophilic and eurytopic arthropods and of arthropods common to temporary and perennial sites did not differ between flow regimes, but were higher during flowing periods, except for xerophilic arthropods. Abundance of hygrophilic arthropods was higher at temporary sites and higher during flowing periods. Sediment moisture content did not differ between perennial and temporary sites, but was higher during flowing periods. There was no interaction between flow regimes and hydrological periods for all measured variables (**Table 1, Figure 3**).

Effect of river drying on community composition

Community composition differed between the temporary and perennial sites only during the dry period (ANOSIM, $F = 1.58$, $R^2 = 0.12$, $p = 0.116$ before the dry period and $F = 2.09$, $R^2 = 0.15$, $p = 0.034$ during the dry period). In addition, the separation of temporary and perennial sites in the two dimensional NMDS plot lower before the dry period (**Figure 4a**) than during the flowing period (**Figure 4b)**. Difference in assemblage composition during the dry period was driven by 1) higher relative abundance or occurrence of *Nargus sp.* (Coleoptera), *Myrmica rubra* (Linnaeus 1758, Formicidae), Staphylininae (Coleoptera) and *Diplostyla concolor* (Wider 1834, Araneae) at temporary sites than perennial sites, and 2) lower relative abundance or occurrence of Formicidae (i.e., *Aphaenogaster subterranean* Latreille 1798, *Temnothorax sp*., *Lasius niger* Linnaeus 1758, *Lasius fuliginosus* Latreille 1798, and *M. graminicola*) at perennial sites (**Figure 4b)**.

Procrustes analysis indicated that the separation of temporary and perennial sites was more pronounced during the dry period compared to before (**Figure 4c**). Arrows representing the differences in site ordination between the hydrological periods of temporary and perennial moved in opposite direction along dimension 1, indicating different temporal changes in community composition. At temporary sites, community composition shifted from dominance (relative abundance and occurrence) by Aleocharinae (Coleoptera), Aphidoidea, Heteroptera and several Araneae species to dominance by Opiliones and *M. graminicola* (Formicidae) (**Table 2**). At perennial sites, community composition shifted from dominance by Oniscidea, *Microneta viaria* (Blackwall 1841, Araneae) and 2 formicidae species to dominance by Opiliones and Diplopoda.

Table 1. Results of the generalized linear models testing the effects of flow regime (temporary versus perennial), hydrological periods (before and during the dry period), and their interaction on the taxonomic richness and abundance of arthropod communities and on sediment moisture content

Dependent variable	Source of variation					
	Flow regime		Period		Flow regime × Period	
	F	*p*	F	*p*	F	*p*
Site richness	15.78	*< 0.01*	46.42	< 0.01	0.29	*0.60*
Site richness, commons	6.32	*0.03*	50.57	< 0.01	0.60	*0.45*
Site richness, predators	7.47	*0.02*	39.43	< 0.01	0.73	*0.41*
Site richness, xerophiles	0.31	*0.59*	3.29	0.10	0.24	*0.64*
Site richness, hygrophiles	10.88	*< 0.01*	29.47	< 0.01	0.11	*0.75*
Site Abundance	3.21	*0.10*	18.14	< 0.01	0.05	*0.83*
Site Abundance, commons	2.61	*0.14*	18.96	< 0.01	0.00	*0.98*
Site Abundance, predators	5.05	*0.04*	28.55	< 0.01	0.04	*0.85*
Site Abundance, xerophiles	0.26	*0.62*	2.05	0.18	0.13	*0.73*
Site Abundance, hygrophiles	6.08	*0.03*	15.16	< 0.01	0.07	*0.79*
Sediment moisture content	0.13	*0.71*	14.42	< 0.01	0.07	*0.78*

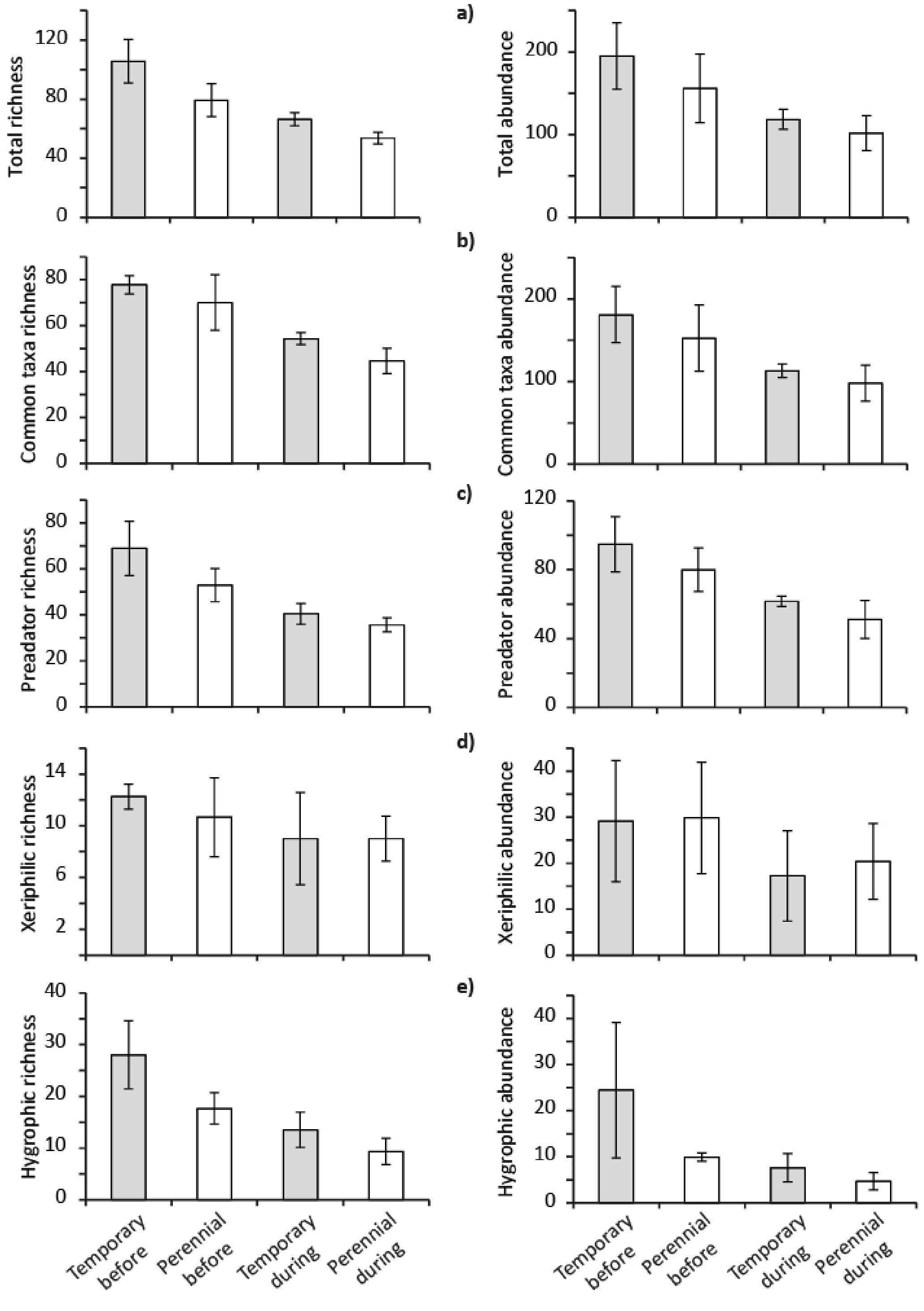

Figure 3 Mean (+ SD) values for taxonomic richness and abundances by flow regimes and hydrological periods. Panel depict a) the all community, b) taxa common to temporary and perennial sites, c) predator taxa, d) xerophilic taxa, e) hygrophilic taxa and f) eurytopic taxa.

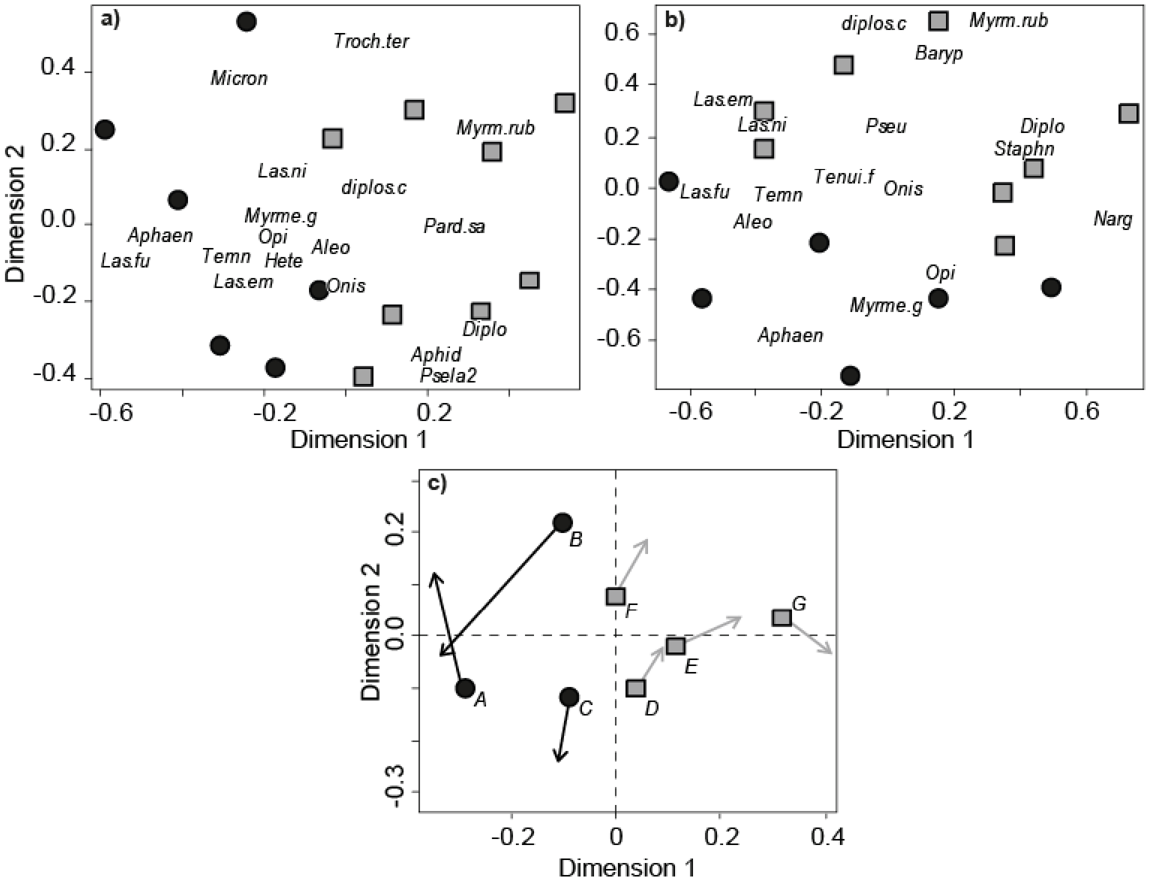

Fig 4. Two-dimensional NMDS plot showing the scores of samples and arthropods collected in the temporary and perennial sites a) before the dry period and b) during the dry period. c) procrustes plots showing temporal variation in NMDS ordination between the 2 hydrological periods. Arrows in c) represent the difference in site ordinations between before (origin of the arrow) and during the dry period (end of the arrow), after data were pooled by hydrological period. Grey squares are temporary sites and dark circles are perennial sites. For clarity, only taxa representing more than 1% of individuals are shown. See supplemental material S1 for taxon codes.

Table 3. Indicator values (%) for taxa collected before and during the dry period at perennial and temporary sites. Taxa with significantly higher indicator values before the dry period are shown in bold type. Only taxa with indicator value > 0.20% and with $p < 0.05$ are shown.

Sites	Taxa	Indicator Value		
Temporary		Before	During	*p*
	Aleocharinae (Coleoptera)	0.45	0.17	0.003
	***Pardosa saltans* (Araneae)**	0.39	0.00	0.001
	Aphidoidea	0.27	0.03	0.001
	***Trochosa terricola* (Thorell 1856, Araneae)**	0.26	0.01	0.001
	***Trochosa ruricola* (De Geer 1778 Araneae)**	0.21	0.00	0.001
	Heteroptera	0.21	0.04	0.019
	***Barypeithes pellicidus* (Boheman, 1834 Coleoptera)**	0.20	0.00	0.001
	Opiliones	0.05	0.39	0.001
	Myrmecina graminicola (Latreille 1802, Formicidae)	0.05	0.29	0.002
Perennial				
	Oniscidea	0.47	0.20	0.044
	***Temnothorax sp.* (Formicidae)**	0.35	0.06	0.003
	***Lasius emarginatus* (Olivier, 1792 Formicidae)**	0.25	0.01	0.002
	***Microneta viaria* (Blackwall 1841Araneae)**	0.20	0.00	0.001
	Opiliones	0.16	0.35	0.048
	Diplopoda	0.01	0.23	0.001

Temporal variability of community composition and cumulative taxonomic richness

Dissimilarity in arthropod community composition among sampling dates did not differ between perennial and temporary sites (**Figure 5,** d.f. = 6, F = 0.20, $p = 0.969$), indicating that the compositional variation of arthropod communities was not higher at temporary sites than at perennial sites.

Rarefaction curves showed that temporary sites accumulated more taxa and more rapidly than perennial sites during the entire study period, as indicated by the absence of overlap of CIs (**Figure 6**). The cumulative taxonomic richness was not significantly different between sites only at the temporary site F. On average, temporary sites contained 1.3 times more taxa than perennial sites.

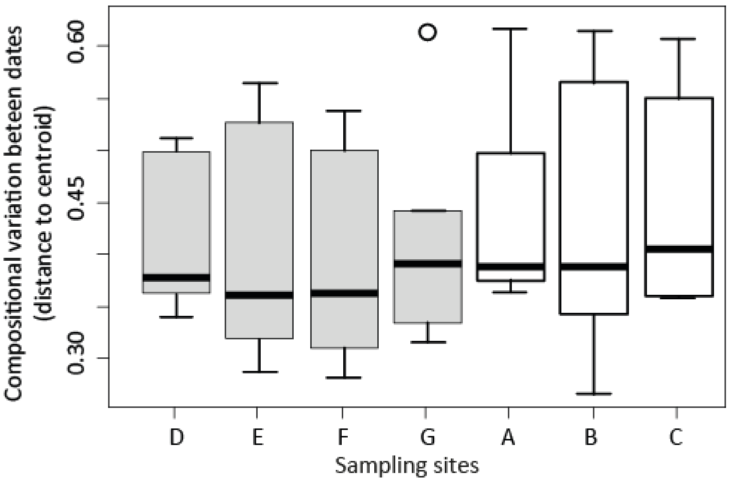

Figure 5. Compositional dissimilarity among sampling dates by sites. Values on the y-axis represent site distances to the group centroid, indicating compositional variatbility within that group. Grey boxplots are temporary sites and white boxplots are perennial sites.

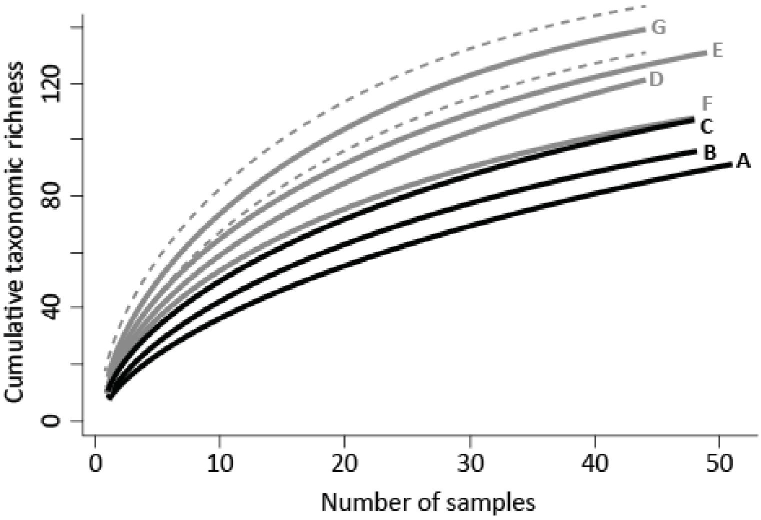

Figure 6 Rarefaction curves scaled to the number of samples for terrestrial arthropods collected in temporary sites (in grey) and perennial sites (in black). For clarity, 95% CIs (grey dotted lines) are shown only for site G. Widths of CIs are similar for other sites. Capital letters indicate site names.

DISCUSSION

River water and aquatic prey subsidies cascade into the adjacent riparian ecosystems due to their use by terrestrial arthropod consumers, elevating *in situ* production in recipient food webs through arrays of direct and indirect interaction (Polis *et al.* 1997, Marczak *et al.* 2007). This study examined the effect of river drying and subsequent disappearance of water resource and aquatic prey subsidies on riparian arthropod communities. First, our results demonstrated that while there was no direct effect of river drying on taxonomic richness and abundance of riparian arthropods, alternating drying and rewetting cycles modified community composition. Second, our results demonstrated that cumulative taxonomic richness was highest at temporary sites although compositional variation of arthropod communities was not lower at perennial sites.

Riparian arthropods during dry periods

Our result did not support our first prediction that taxonomic richness and abundance of terrestrial arthropods would be lowest at temporary sites during dry periods as a result of cascading effects of river drying on riparian predators and hygrophilous species. Rather, we found similar temporal biodiversity patterns at both perennial and temporary sites. In addition, the diversity and abundance of arthropods were still high during the dry period compared to before. This indicates water resource and aquatic prey availability were not the main factors driving arthropod populations in the riparian zone of the Albarine River, in contrast to awith previous study in a dryland river of Arizona (McCluney and Sabo 2012). The authors found lower riparian taxonomic richness during drying events and suggested the availability of drinking water was the primary factor determining riparian communities. In the Albarine River, we found no difference in sediment moisture content between temporary and perennial sites. Rains, dew and vegetation cover likely maintained sufficient moisture for arthropods thereby compensating for the disappearance of drinking water. In addition, sufficient inputs of rainwater combined with hot summer temperature stimulate a pulse in primary production (Xu *et al.* 2004) which could support primary consumers. Dry riverbeds also constitute supplementary habitats for riparian arthropods (Wishart 2000, Steward *et al.* 2011, Corti *et al. in prep*) and could supply additional food resources such as young shoots and micro-organisms and reduce competition for resources in riparian zones (Corti *et al. in prep*). Whereas most of the studies reporting that river drying alters riparian communities have been realized in arid regions (*e.g.* Stromberg *et al.* 2009, Hagen & Sabo 2012, Katz *et al.* 2012, McKunley and Sabo 2012), we contend that community responses to drying vary among climatic regions. Depending on their intensity, the responses of riparian communities may decrease trophic interactions and possibly alter food chain dynamic.

At both the temporary and perennial sites, taxonomic richness and abundance of riparian arthropods decreased during the study period indicating organism activity is synchronized with environmental changes. In particular, most of hygrophilic species (*e.g. Microneta varia* (Araneae), *Parenchus albipes* (Carabidae), *Lasius platythorax* (Formicidae)) disappeared during the dry period at all sites. Arthropods in nature exhibit strong seasonal variations in activity patterns (Uetz 1976, Lovei & Sunderland 1996). Activity density of most species peaks in spring then decreases until winter which corresponds to the hibernation or diapause stage. One possible explanation of this pattern is that arthropod activity is synchronized with resource availability. For example, Paetzold *et al.* (2006) have shown that taxonomic richness and density of riparian predators peak corresponding with high abundance of emergent aquatic insects. Therefore, the decrease in taxonomic richness and abundance observed in this study is due to the fact that the summer-autumn dry periods in the Albarine River match with the period of low activity for arthropods. Such matching of activity patterns with unfavorable seasonal conditions could be a resistance strategy, because several arthropods may have completed their life cycle before summer and are prepared for subsequent hibernation (Lovei & Sunderland 1996). Life-history traits may thus favor the capacity of riparian arthropods to tolerate the decrease in water resource and the absence of aquatic subsidies during river drying. As a consequence, the timing of dry periods is likely an important factor controlling the responses of riparian arthropods to river drying. Dry events occurring during late summer or winter could have less effect than spring dry events, when most of the taxa peak in density. Many once-perennial rivers are running dry because of excessive water abstraction and climate change while natural temporary rivers are expected to suffer from longer and intense dry periods (Gleick 2003, Larned *et al.* 2010, Döll & Müller Schmied 2012). We expect that riparian arthropods could show high resistance to shifts from perennial to temporary flow regimes under temperate climates. In spite of this, arthropod communities could be severely affected by human activities that advance drying events earlier in the hydrological season. The numerous uncommon and vulnerable arthropods that are highly adapted to conditions in riparian habitats (Sadler *et al.* 2004, Andersen & Hanssen 2005) could be the most affected species.

Alternating drying and rewetting cycles alter community composition

Whereas no difference in community composition between temporary and perennial sites was found before the dry period, community composition strongly diverged when the river ran dry. Yet, the extent of temporal variations in taxonomic richness, abundance and composition were similar at both sites indicating each gained and lost different taxa during the dry period. Dissimilarity in individual activity patterns and diet regime can explain patterns of species loss and gain. For example, taxa have been shown to respond differently to subsidy variations in relation to their specialization on aquatic subsidies: ground beetles with a diet consisting predominantly of aquatic insects responded strongly to subsidy reductions, while lycosid spiders with no particular diet showed no significant response (Paetzold *et al.* 2006). At perennial sites, aquatic insect emergence could allow the establishment of riparian species with dependence on aquatic subsidies and summer and autumn activity patterns. More importantly, taxa turnover at temporary sites indicates that river drying does not create poor quality environments but rather benefits to colonists from other terrestrial habitats. As a consequence, temporary and perennial sites in the Albarine River both contribute substantially to regional arthropod biodiversity. From a conservation perspective, much effort is needed to understand how temporary and perennial flow conditions determine the presence-absence of “valued” species and to quantify much they contribute to regional diversity.

The effects of river drying on riparian arthropods are probably leveled off during subsequent flowing periods because no difference in community composition was observed before the dry period between temporary and perennial sites. Upon flow resumption, species previously affected by river drying can probably quickly recolonize temporary sites using both resistance and resilience traits. Resistance includes the ability of taxa to survive to the dry period in temporary sites into hibernation or diapause stages (Andersen 1985). Resilience traits are mainly due to dispersion abilities through flight and ballooning (Desender 1989, Bates *et al.* 2007). Periodical floods could also be act as a dispersal mechanism (Corti & Datry 2012). Numerous studies have reported that riparian arthropods exhibit numerous strategies to resist to inundation (Boumezzough & Musso 1983, Lambeets *et al.* 2008b) and numerous living arthropods have been collected in a temporary river during a rewetting event (Corti & Datry 2012). Accordingly, resilience of arthropod communities to river drying may vary with the position of temporary sections across river networks. For instance, riparian communities in the temporary reaches of headwater streams may have a much lower resilience than those of downstream temporary sections. However, the effect of contrasted fragmentation patterns of aquatic habitats on riparian communities is still unexplored.

Communities are richer at temporary than perennial sites

Our third prediction that drying and rewetting cycles in rivers increase temporal variability of community composition and hence resulting in higher cumulative taxonomic richness at temporary sites was not supported by the results. Temporal turnover was similar at temporary and perennial sites whereas communities were richer both before and during the dry period at temporary sites. This is inconsistent with results reported from arid regions, where a lower taxonomic richness of plants and arthropods is generally observed at temporary sites or rivers (Stromberg *et al.* 2009, Katz *et al.* 2012, McCluney & Sabo 2012). In the Albarine River, the presence at temporary sites of both typical riparian species and colonists from other terrestrial habitats leads to a high diversity. Although terrestrial arthropods have high dispersal ability that enables them to respond quickly to spatial and temporal changes and locate suitable habitats (Bates *et al.* 2007), dispersal can have a cost. For example, there is a greater mortality risk during dispersal due to increased energy expenditure, unfamiliar habitat, or predation risk (Johnson *et al.* 2009). Therefore, part of temporary site colonists may have strategies allowing them to resist flowing periods in the same way as typical riparian species resist dry periods.

Shorter food chain length in temporary rivers compared to perennial rivers could also contribute to the high taxonomic richness and abundance of riparian arthropods observed in this study. For example, emerging aquatic insects subsidized insectivorous riparian birds along a Japanese stream (Murakami and Nakano 2002). The resulting increase in bird abundance magnified top–down control of terrestrial insects in the riparian forest relative to the unsubsidized upland forests. In temporary rivers, one may expect that such a top-down control does not exist. Since temporary rivers exhibit low aquatic invertebrate density (Arscott *et al.* 2010, Datry 2012), the absence of pulse in aquatic subsidies during emergence periods may result in lower abundance of insectivorous predators such as birds, bats and lizards. In turn, this may favor the growth of riparian populations, insofar as terrestrial resources allow them to be self-sufficient in the absence of aquatic subsidies. This would indicate that factors affecting invertebrate productivity in temporary rivers drive food web dynamics in adjacent riparian food webs by altering energy flux across ecosystem boundaries in several trophic levels. Aquatic-terrestrial linkages and food web dynamic in riparian ecosystems have been mostly studied in response to pulses or declines in aquatic subsidies (Sanzone *et al.* 2003, Paetzold *et al.* 2008, Akamatsu & Toda 2011). Our results suggest that river drying has complex and interrelated effects on riparian communities and trophic interactions. Temporary rivers thus constitute experimental, natural laboratories where aquatic subsidies can be manipulated allowing the study of tangled food webs. More generally, they represent good models to gain insight into aquatic-terrestrial linkages and energy transfer across ecosystem boundaries.

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Supplementary material S1 Total of individuals (Sum), percentage of occurrence (Occ) feeding guilds, ecological groups and abbreviations of taxa collected at temporary (T) and perennial (P) sites. PP: predator/polyphagous, Ph: phytophagous, D: detritivorous. h: hygrophilic, eu: eurytopic and x: xerophylic arthropods

Taxa		Abbrev	Secteur	Guild	Group	Sum	Occ
ARACHNIDA							
Araneae							
Agelenidae	*Histopona torpida*	Histo	T	PP	h	7	0.17
	Inermocoelotes inermis	Inermo	T	PP	eu	6	0.11
	Malthonica silvestris	Malth.s	T	PP	eu	28	0.52
	Tegenaria agrestis	Tege.ag	T	PP	h	1	0.03
Amaurobiidae	*Coelotes terrestris*	Coel.t	T	PP	eu	1	0.03
Atypidae	*Atypus affinis*	Atyp	P	PP	x	1	0.03
Clubionidae	*Clubiona comta*	Club.c	P	PP	h	4	0.11
	Clubiona lutescens	Club.l	P	PP	h	2	0.06
	Clubiona terrestris	Club.t	T.P	PP	h	10	0.23
Corinnidae	*Phrurolithus festivus*	Phrur.f	T.P	PP	eu	21	0.37
Corinnidae	*Phrurolithus minimus*	Phrur.m	T.P	PP	x	4	0.09
Dysderidae	*Dysdera erythrina*	Dysd.e	T.P	PP	x	22	0.52
	Harpactea hombergi	harpac	T	PP	eu	3	0.09
Gnaphosidae	*Drassyllus praeficus*	Drassy.pr	T	PP	x	1	0.03
	Micaria pulicaria	Mica.pu	T.P	PP	h	3	0.09
	Trachyzelotes pedestris	Trachy	T.P	PP	eu	15	0.29
	Zelotes apricorum	Zel.ap	T.P	PP	eu	5	0.14
	Zelotes latreillei	Zel.la	P	PP	eu	2	0.06
Hahniidae	*Antistea elegans*	Antist	T	PP	h	1	0.03
	Hahnia montana	Hahn.m	T	PP	h	2	0.03
	Hahnia pusilla	Hahn.p	T	PP	eu	1	0.03
Linyphiidae	*Bathyphantes gracilis*	Bathy.g	P	PP	h	2	0.06
	Bathyphantes nigrinus	Bathy.n	P	PP	h	2	0.03
	Centromerita bicolor	Centro.b	P	PP	h	1	0.03
	Centromerus sylvaticus	Centro.sy	T.P	PP	h	22	0.60
	Collinsia distincta	Colli.d	P	PP	h	1	0.03
	Dicymbium tibiale	Dicy.t	P	PP	h	2	0.06
	Diplocephalus cristatus	Dipl.c	T.P	PP	h	36	0.74
	Diplocephalus latifrons	Dipl.l	T	PP	h	1	0.03
	Diplocephalus picinus	Dipl.p	T.P	PP	h	4	0.11
	Diplostyla concolor	diplos.c	T.P	PP	h	199	2.38
	Gongylidium rufipes	Gon.r	P	PP	h	2	0.06
	Lessertinella kulczynskii	Lessert	P	PP	h	1	0.03
	Macrargus rufus	Macrar	P	PP	eu	1	0.03
	Meioneta affinis	Meio	P	PP	eu	1	0.03
	Mermessus trilobatus	Merm.t	T.P	PP	x	3	0.09
	Micrargus herbigradus	Micra.h	P	PP	eu	1	0.03
	Microneta viaria	Micron	T.P	PP	h	97	0.97
	Neriene clathrata	Nerie	P	PP	h	2	0.06
	Oedothorax agrestis	Oedo.ag	T.P	PP	h	4	0.09
	Oedothorax apicatus	Oedo.ap	T.P	PP	h	5	0.11
	Oedothorax retusus	Oedo.er	T.P	PP	h	22	0.32
	Palliduphantes pallidus	Pallidu	T.P	PP	eu	14	0.37
	Porrhomma microphtalmum	Porrh.n	T	PP	h	1	0.03
	Silometopus elegans	Silo.e	P	PP	h	1	0.03
	Sintula corniger	Sint	P	PP	eu	2	0.06
	Syedra gracilis	Sye.g	P	PP	eu	1	0.03

Taxa		Abbrev	Secteur	Guild	Group	Sum	Occ
	Tenuiphantes cristatus	Tenui.cr	T	PP	h	3	0.06
	Tenuiphantes flavipes	Tenui.f	T.P	PP	eu	103	1.83
	Tenuiphantes tenuis	Tenui.te	P	PP	eu	12	0.34
	Tenuiphantes zimmermanni	Tenui.zi	T	PP	h	2	0.03
	Troxochrus scabriculus	Troxoc	T.P	PP	h	40	0.63
	Walckenaeria acuminata	Walc.ac	T.P	PP	eu	6	0.14
	Walckenaeria atrotibialis	Walct	P	PP	h	2	0.06
	Walckenaeria cuspidata	Walc.cu	T	PP	h	1	0.03
	Walckenaeria nudipalpis	Walc.nu	P	PP	h	9	0.23
	Walckenaeria obtusa	Walc.ob	T	PP	h	4	0.11
Liocranidae	*Liocranoeca striata*	Liocr	P	PP	eu	4	0.11
	Scotina celans	Scot	T.P	PP	eu	16	0.09
Lycosidae	*Aulonia albimana*	Aulo	T.P	PP	eu	8	0.14
	Pardosa amentata	Pard.am	T.P	PP	h	61	0.46
	Pardosa hortensis	Pard.hor	T.P	PP	eu	58	0.69
	Pardosa morosa	Pard.mo	P	PP	h	2	0.06
	Pardosa prativaga	Pard.pra	P	PP	h	7	0.20
	Pardosa proxima	Pard.pro	P	PP	h	2	0.06
	Pardosa pullata	Pard.pul	P	PP	eu	1	0.03
	Pardosa saltans	Pard.sa	T.P	PP	x	97	1.43
	Piratula hygrophila	Pira.hy	P	PP	h	35	0.40
	Piratula knorri	Pira.kn	T	PP	h	22	0.14
	Piratula latitans	Pira.la	T.P	PP	h	3	0.09
	Trochosa ruricola	Troch.ru	T.P	PP	eu	44	0.63
	Trochosa terricola	Troch.ter	T.P	PP	eu	108	1.40
Mimetidae	*Ero furcata*	Ero.f	P	PP	eu	2	0.06
Pisauridae	*Pisaura mirabilis*	Pis.m	P	PP	eu	2	0.06
Salticidae	*Myrmarachne formicaria*	Myrma	P	PP	eu	1	0.03
	Neon reticulatus	Neon	T.P	PP	h	3	0.09
Tetragnathidae	*Pachygnatha degeeri*	Pachy.d	P	PP	eu	4	0.03
Theridiidae	*Crustulina guttata*	Crus.g	T	PP	eu	1	0.03
	Episinus truncatus	Epi.t	T	PP	x	1	0.03
	Euophrys frontalis	Euo.f	P	PP	eu	2	0.06
	Euryopis flavomaculata	Eur.f	P	PP	eu	8	0.20
	Robertus lividus	Rob.l	P	PP	h	4	0.09
	Robertus neglectus	Rob.n	P	PP	h	1	0.03
Thomisidae	*Ozyptila atomaria*	Ozy.at	T	PP	eu	1	0.03
	Ozyptila praticola	Ozy.pr	T.P	PP	h	12	0.26
Zodariidae	*Zodarion italicum*	Zod.it	T.P	PP	x	58	0.69
	Zora spinimana	Zora.sp	T.P	PP	eu	13	0.37
Opiliones		Opi	T.P	PP	NA	356	3.98
Pseudoscorpionida		Pseu	T.P	PP	NA	122	2,29
CHILOPODA		Chilo	T.P	PP	NA	71	1.72
DIPLOPODA		Diplo	T.P	D	NA	235	2.32
Iulidae		Iul	T.P	Ph	NA	97	1.38
DIPLURA		Diplu	T.P	PP	NA	3	0.06
INSECTA							
Archaeognatha		Archa	T.P	Ph	NA	107	1,26
Blattoptera		Blatt	T.P	PP	NA	4	0.11
Coleoptera							
Anobiidae		Ano	P	Ph	NA	1	0.03
	Anobium hederae	Ano.h	P	Ph	NA	1	0.03
Anthicidae	*Anthicus antherinus*	Anthnt	T.P	PP	eu	16	0.11
	Endomia occipitalis	Endo.o	P	PP	NA	7	0.17

Taxa		Abbrev	Secteur	Guild	Group	Sum	Occ
Aphodiidae	*Melinopterus sp.1*	Meli	P	D	NA	2	0.06
Buprestidae	*Trachys fragariae*	Trachys.f	P	Ph	x	1	0.03
Byrrhidae	Byrrhidae sp.1	Byrr	P	Ph	NA	4	0.09
	Porcinolus murinus	Por.m	P	Ph	x	1	0.03
Carabidae	*Agonum spp.*	Ago	P	PP	h	10	0.17
	Amara eurynota	Amar	P	Ph	x	12	0.26
	Anchomenus dorsalis	Ancho	P	PP	x	69	0.49
	Anthracus consputus	Anthra	T.P	PP	h	34	0.63
	Asaphidion spp.	Asaph	T.P	PP	NA	5	0.14
	Badister bullatus	Badis	P	PP	h	6	0.17
	Bembidion quadrimuculatum	Bemb.q	P	PP	x	4	0.06
	Blemus discus	Blem.d	P	PP	eu	1	0.03
	Carabidae sp.1	Cara1	P	PP	NA	17	0.2
	Carabidae sp.2	Cara2	P	PP	NA	14	0.17
	Carabidae sp.3	Cara3	P	PP	NA	3	0.09
	Carabus auratus	Carau	P	PP	x	14	0.23
	Carabus coriaceus	Cara.cor	T.P	PP	eu	16	0.4
	Carabus nemoralis	Cara.n	T.P	PP	h	4	0.11
	Clivina collaris	Cliv.c	P	PP	eu	5	0.09
	Leistus fulvibarbis	Leis.f	P	PP	h	1	0.03
	Metallina lampros	Metal.l	T.P	PP	x	4	0.09
	Nebria brevicollis	Neb.b	T.P	PP	h	17	0.09
	Notiophilus sp.	Notio	T.P	PP	x	4	0.11
	Ocydromus atrocoeruleus	Ocyd	P	PP	h	1	0.03
	Ocydromus complanatus	Ocyd.com	T	PP	h	1	0.03
	Ocydromus decorus	Ocyd.d	T.P	PP	h	5	0.09
	Ocydromus femoratus	Ocyd.f	T.P	PP	h	25	0.29
	Ocydromus testaceus	Ocyd.tes	P	PP	h	13	0.17
	Ocydromus tetragrammus	Ocyd.t	T.P	PP	NA	25	0.37
	Ophonus sp.1	Opho1	T.P	Ph	NA	2	0.06
	Oxypselaphus obscurus	Oxy.o	P	PP	h	2	0.03
	Panagaeus sp.1	Pana1	P	PP	NA	1	0.03
	Paranchus albipes	Paran	T.P	PP	h	49	0.66
	Platynus assimilis	Platy	P	PP	h	1	0.03
	Poecilus spp.	Poe	P	PP	h	7	0.06
	Pterostichus cristatus	Pte.c	P	PP	h	1	0.03
	Pterostichus madidus	Pte.ma	T.P	PP	eu	10	0.26
	Pterostichus melanarius	Pte.me	P	PP	eu	2	0.03
	Pterostichus sp.1	Pte1	T.P	PP	NA	6	0.17
	Pterostichus vernalis	Pte.v	P	PP	h	8	0.11
	Stomis pumicatus	Sto.p	T.P	PP	h	7	0.17
	Syntomus obscuroguttatus	Synt.o	P	PP	h	1	0.03
	Tachys bistriatus	Tac.b	P	PP	h	4	0.11
	Tachyura spp.	Tachyu	P	PP	NA	1	0.03
	Trechus obtusus	Tre.o	T.P	Ph	eu	4	0.11
	Trechus quadristriatus	Tre.q	P	PP	x	29	0.49
Cerambycidae	*Grammoptera ruficornis*	Gram.r	P	Ph	x	1	0.03
Chrysomelidae	*Aphthona venustula*	Aphth	T	Ph	eu	1	0.03
	Asiorestia ferruginea	Asio	T	Ph	eu	8	0.03
	Chaetocnema sp.	Chaet	T.P	Ph	eu	31	0.23
	Chrysomelidae sp.1	Chryso1	P	Ph	NA	2	0.06
	Crepidodera sp.	Crepi	T.P	Ph	NA	8	0.14
	Longitarsus spp.	Long	T.P	Ph	NA	8	0.2
	Oomorphus concolor	Oom.c	T.P	Ph	eu	20	0.49

Taxa		Abbrev	Secteur	Guild	Group	Sum	Occ
	Phyllotreta spp.	Phy	P	Ph	NA	26	0.37
	Pyrrhalta viburni	Pyrr.v	T.P	Ph	h	2	0.06
Ciidae		Ciid	T.P	Ph	NA	3	0.09
Clambidae	*Clambus sp.*	Clamb	T.P	D	NA	25	0.52
Coccinellidae	*Tytthaspis sedecimpunctata*	Tytth.s	P	Ph	x	1	0.03
	Vibidia duodecimguttata	Vibi	P	Ph	h	1	0.03
Corylophidae	*Sericoderus lateralis*	Seric.l	P	Ph	NA	3	0.09
Cryptophagidae	*Atomaria sp.*	Ato	T.P	Ph	NA	70	1.17
	Caenoscelis sp.	Caenos	P	Ph	NA	11	0.14
	Cryptophagus sp.	Crypt	T.P	Ph	NA	43	0.74
Curculionidae	*Acalles spp.*	Acall	T.P	Ph	NA	21	0.54
	Adexius scrobipennis	Adex.s	T.P	Ph	NA	4	0.11
	Archarius sp.1	Archa1	P	Ph	NA	10	0.2
	Aulacobaris coerulescens	Aulaco.c	P	Ph	eu	1	0.03
	Barypeithes pellicidus	Baryp	T.P	Ph	eu	111	1.06
	Brachysomus hirtus	Brachy.h	P	Ph	NA	1	0.03
	Donus sp.	Don	T.P	Ph	NA	3	0.09
	Dorytomus	Dory	P	Ph	NA	1	0.03
	Hemitrichapion reflexum	Hemit.ref	P	Ph	NA	1	0.03
	Otiorhynchus rugosostriatus	Otio.r	P	Ph	NA	2	0.06
	Polydrusus sericeus	Polyd.s	P	Ph	NA	1	0.03
	Cossonus sp.1	Cosso	T	Ph	NA	1	0.03
	Cotaster uncipes	Cata.u	T.P	Ph	NA	8	0.23
	Curculionidae sp.1	Cucu1	T.P	Ph	NA	3	0.06
Drilidae	*Drilus flavescens*	Dril.f	P	PP	eu	1	0.03
Dryopidae	*Dryops ernesti*	Dryo.e	T	D	NA	2	0.06
	Esolus sp.	Eso	T.P	D	h	21	0.2
	Limnius volckmari	Limn.v	T	D	h	6	0.11
	Pomatinus substriatus	Poma.s	P	D	h	2	0.06
Dynastinae	*Bothynus sp.*	Bothy	T.P	D	NA	3	0.09
Elateridae	*Agriotes sp*	Agrio	T.P	Ph	NA	4	0.11
	Zorochros dermestoides	Zoro.d	T.P	Ph	eu	80	0.69
Elmidae	*Elmis aenea*	Elm	T	D	h	2	0.06
Hydraenidae	*Hydraena gracilis*	Hydr.g	T	NA	h	1	0.03
Hydrophilidae	*Cercyon sp.*	Cercy	T.P	D	NA	14	0.37
	Georissus crenulatus	Geori.c	T.P	PP	h	13	0.2
Lampyridae		Lamp	T.P	PP	NA	9	0.26
Latridiidae	*Corticaria spp.*	Corti2	T.P	Ph	NA	7	0.17
	Corticarina spp.	Corti1	T.P	Ph	NA	14	0.32
Leiodidae	*Catops fuliginosus*	Catops.f	T.P	D	NA	8	0.2
	Colenis immunda	Colen.i	T.P	D	NA	4	0.11
	Leiodes polita	Leio.p	T.P	D	NA	6	0.17
	Nargus spp.	Narg	T.P	D	NA	72	0.66
	Ptomaphagus sp.	Ptom	T.P	D	NA	33	0.6
	Sciodrepoides watsoni	Scio.w	T.P	D	NA	20	0.29
Meloidae	Meloidae sp.1	Meloi	T	PP	NA	1	0.03
Pselaphidae	Pselaphinae spp.	Psela2	T.P	PP	NA	128	1.49
	Pselaphus heisei	Psela.h	T	PP	NA	1	0.03
Scarabaeidae	*Serica brunnea*	Ser.b	T	D	eu	1	0.03
Scolytidae	*Xyleborus dispar*	Xyle.d	T	Ph	NA	1	0.03
Scydmaenidae	*Stenichnus collaris*	Ste.c	T.P	PP	h	4	0.11
Silphidae		Silph	P	D	NA	1	0.03
	Phosphuga atrata	Phos	T.P	PP	eu	16	0.34
Staphylinidae	Aleocharinae	Aleo	T.P	NA	NA	984	5.33

Taxa		Abbrev	Secteur	Guild	Group	Sum	Occ
	Ancyrophorus flexuosus	Ancyr.f	P	D	NA	24	0.17
	Anthobium atrocephalum	Anthob	T.P	NA	NA	5	0.14
	Astenus sp.	Ast	P	NA	NA	1	0.03
	Deleaster dichrous	Delea.d	P	NA	NA	1	0.03
	Micropeplus sp.1	Microp	P	D	NA	1	0.03
	Mycetoporus spp.	Myce	T.P	Ph	NA	9	0.2
	Omalium spp.	Oma	T.P	NA	NA	13	0.37
	Oxytelinae	Oxyt	T.P	D	NA	46	1
	Paedericus spp.	Paed1	P	PP	h	2	0.03
	Paederinae spp.	Paed2	P	PP	h	2	0.06
	Paederus spp.	Paed	T.P	PP	h	11	0.32
	Proteinus spp.	Prot	T.P	PP	NA	5	0.11
	Staphylininae spp.	Staphn	T.P	D	NA	96	1.69
	Stenus spp.	Ste	T.P	PP	h	75	1.66
	Tachyporinae spp.	Tach	T.P	Ph	NA	26	0.6
	Xantholinae spp.	Xanth	T.P	PP	NA	10	0.26
Dermaptera		Derm	T.P	PP	NA	9	0.17
Hemiptera		Hemi.A	T.P	PP	NA	35	0.8
Aphidoidea		Aphid	T.P	Ph	NA	158	1.63
Cicadellidae		Cica	T.P	Ph	NA	33	0.52
Heteroptera		Hete	T.P	PP	NA	109	1.78
Hymenoptera							
Formicidae	*Aphaenogaster subterranea*	Aphaen	T.P	PP	x	257	2.09
	Camponotus truncatus	Camp.t	T	NA	x	1	0.03
	Chthonolasius sp.	Chton	T.P	PP	NA	4	0.09
	Formica gagates	Form.g	T.P	PP	NA	2	0.06
	Lasius brunneus	Las.br	T.P	PP	x	42	0.49
	Lasius emarginatus	Las.em	T.P	PP	x	353	1.6
	Lasius flavus	Las.fl	T.P	PP	x	15	0.2
	Lasius fuliginosus	Las.fu	T.P	PP	eu	733	1.26
	Lasius niger	Las.ni	T.P	PP	x	755	2.32
	Lasius paralienus	Las pa	T.P	PP	x	6	0.14
	Lasius platythorax	Las.pl	T.P	PP	h	43	0.63
	Lasius sp.1	las1	T.P	PP	NA	9	0.23
	Lasius sp.2	las2	T	PP	NA	1	0.03
	Myrmecina graminicola	Myrme.g	T.P	PP	x	230	3.04
	Myrmica rubra	Myrm.rub	T.P	PP	eu	502	2.92
	Myrmica ruginodis	Myrm.rug	T.P	PP	eu	21	0.43
	Myrmica sabuleti	Myrmsa	T	PP	x	2	0.03
	Myrmica sp.1	Myrm1	T.P	PP	eu	11	0.2
	Ponera sp.	Pon	T.P	PP	NA	2	0.06
	stenamma debile	stena	T.P	NA	eu	17	0.26
	Tapinoma sp.	Tapi	P	PP	x	1	0.03
	Temnothorax sp.	Temn	T.P	PP	NA	327	3.01
	tetramorium sp.	tetra	T.P	PP	x	28	0.32
Orthoptera		Orth	P	D	NA	1	0.03
Gryllidae		Gryll	T	PP	NA	3	0.06
Siphonaptera		Siph	T.P	Parasites	NA	62	1,03
MALACOSTRACA							
Oniscidea		Onis	T.P	D	NA	3350	7.16

6

FLUX D’INVERTEBRES ET DE MATIERE ORGANIQUE DANS UN FRONT DE REMISEN EAU

Article 4

Invertebrates and sestonic matter in an advancing wetted front travelling down a dry river bed (Albarine, France)

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ABSTRACT

Temporary rivers are shifting mosaics of aquatic and terrestrial habitat driven by hydrologic variability. Advancing wetted fronts (AWFs) that rewet dry river beds are unpredictable events, and knowledge about their composition and role in habitat mosaics is scarce. We collected dead and living terrestrial invertebrates, aquatic invertebrates, and sestonic matter (i.e., suspended sediments and organic matter) entrained by flow in an AWF travelling downstream over a 7-km-long dry reach. We collected samples at 12 sites along the rewetting reach and at 3 sites in the upstream perennial reach of the Albarine River, France. Invertebrates in the AWF were mainly of terrestrial origin and organic matter was essentially coarse (>5 mm). Terrestrial invertebrate density and taxonomic richness and sestonic matter concentration were several orders of magnitude higher in the AWF than in the perennial reach. However, only terrestrial invertebrate taxonomic richness increased longitudinally. At least ⅓ of terrestrial taxa could have survived submersion, and the density and taxonomic richness of these taxa decreased downstream. These results indicate that terrestrially-derived material is stored downstream during rewetting where it could greatly stimulate instream aquatic productivity and succession in terrestrial invertebrates along the riparian zone. In contrast, entrained aquatic taxa represented ~15% of the benthic taxa collected 1 mo month after rewetting, indicating a low contribution of AWFs to benthic invertebrate succession. In the context of global change and increasing appropriation of water resources by humans, our results suggest that conceptual models of invertebrate dynamic and organic matter processing in rivers should account for dry phases and transitional periods from dry to wet conditions.

Key-words: Temporary rivers, flash flood, aquatic and terrestrial arthropods, organic matter, pulse.

INTRODUCTION

In temporary rivers, hydrologic variability generates shifting mosaics of terrestrial and aquatic habitat, accommodating diverse terrestrial and aquatic communities across river networks (Larned *et al.* 2010). During drying periods, terrestrial habitats expand by retreating wetted fronts (RWFs) that progress longitudinally in the upstream or downstream direction, creating chains of disconnected pools and eventually leading to complete riverbed drying (Lake 2003). RWFs can occur simultaneously at several reaches depending on geomorphic context and the presence of constrained and unconstrained reaches (Stanley *et al.* 1997). Continuous flow is reestablished when flow pulses trigger advancing wetted fronts (AWFs), which expand aquatic habitats to the detriment of terrestrial ones (Jacobson *et al.* 2000).

Expansion and contraction of aquatic and terrestrial habitats are immediately followed by the colonization, emigration, or death of invertebrate species. RWFs and the contraction of aquatic habitats induce some benthic species to emerge or escape to perennial refuges, whereas others die within a few hours or days stranded on the dry river beds and some persist in dry sediments as desiccation-resistant forms for weeks or months (Stubbington *et al.* 2009, Datry *et al.* 2012). At the same time, expanding terrestrial habitats are being colonized by terrestrial invertebrates (*e.g.* Collembola, Lycosidae, Chrysomelidae and Formicidae) originating mostly from adjacent riparian areas (Steward *et al.* 2011, RC, personal observation). Recent evidence suggests that terrestrial assemblages in dry river beds could be highly diverse (Wishart 2000, Corti *et al.* 2011, Steward *et al.* 2011). However, little is known about the fate of these organisms during rewetting, and the influence of AWFs on benthic and terrestrial ground-dwelling invertebrates has been largely unexplored.

AWFs are sudden and unpredictable events. They can take the form of flood bores or expanding pools of upwelling groundwater (Reid *et al.* 1998, Doering *et al.* 2007). The former are the most frequently reported AWFs, and their energy and potential rapidity can be remarkable (Jahns 1949). Descriptions of flood bores travelling forward over dry river beds are often spectacular. The sound of gravel and stones clanging together can be audible over distances greater than 100 m (Jahns 1949). The flow is highly turbulent, and AWF velocity can be as high as 3 m/s, with most frequent values in the range of 1 to 2 m/s (Jahns 1949, Reid *et* *al.* 1998, Dunkerley and Brown 1999, Jacobson *et al.* 2000, Doering *et al.* 2007). AWFs transport large quantities of sestonic matter (i.e., suspended sediments and organic matter) (Larned *et al.* 2010, Jacobson and Jacobson 2012) and their concentrations tend to increase as the flood bore moves downstream (Reid *et al.* 1998, Jacobson *et al.* 2000).

AWFs may entrain terrestrial invertebrates from dry river beds, and therefore, their density may increase as the wetted front travels downstream. However, rewetting may not necessarily be catastrophic for terrestrial invertebrates because some have adaptations that allow them to escape the flood or resist submersion (Boumezzough and Musso 1983, Lytle and Poff 2004, Lambeets *et al.* 2008). Submersion-resistant taxa have been reported from flooded forests and temperate grasslands (Adis and Junk 2002), but not from temporary rivers. In field and laboratory experiments, some riparian Carabidae, Staphylinidae, and Araneae (*e.g. Pardosa agricola, Chlaenius velutinus, Pterostichus lasserei*) have different survival strategies enabling them to persist following submersion. Sheltering and escaping are the 2 dominant strategies during slow increases in water level (Boumezzough and Musso 1983, Lambeets *et al.* 2008). Rapid increases in water level submerge most individuals, but crawling, flotation, and respiration through air bubbles allow some taxa to survive submersion periods of up to 20 h. Concurrently, AWFs may transport aquatic invertebrates from upstream perennial reaches or refuges (*e.g.* remnant pools). Flow pulses increase aquatic invertebrate drift in perennial streams (Matthaei *et al.* 1997), and aquatic invertebrate dispersal may depend on the distance from sources of aquatic colonists (Gore 1982). Therefore, AWFs may contribute to some extent to aquatic invertebrate recovery after rewetting, which is generally quick in temporary rivers (Stanley *et al.* 1994, Datry 2012).

We examined the longitudinal distribution of aquatic and terrestrial invertebrates and seston along an AWF in a temporary river. Our 1st objective was to compare aquatic and terrestrial invertebrate assemblages and sestonic matter concentrations between the AWF and upstream perennial reaches and to assess the capacity of terrestrial taxa to resist submersion. Our 2nd objective was to examine longitudinal changes in the composition of the AWF. Our 3rd objective was to examine the importance of aquatic invertebrates entrained in the AWF as colonists of rewetted benthic habitats. To this end, we measured invertebrate density and seston concentrations in the very first flow pulse of a flood bore travelling 6 km downstream. We sampled the AWF at 12 rewetted sites and at 3 upstream perennial sites. In addition, 36 d after resumption of flow, we collected benthic invertebrates in the river from the same sites.

METHODS

Study site

The Albarine River

The Albarine River drains a 313 km^2 catchment in temperate eastern France (Figure 1A, B). After flowing for 45 km over a karstic plateau and through gorges, the Albarine reaches a 15-km-long alluvial gravel-bed plain before joining the Ain River (Figure 1B). Along this alluvial plain, the river is perched 1 to 14 m above the regional aquifer water table and continuous infiltration of surface water through glaciofluvial deposits leads to a downstream decrease in discharge (Datry *et al.* 2011). As flow decreases during periods of low runoff, a retreating wetted front moves progressively upstream, causing the length of the dry reach to increase. Flow pulses that follow high runoff periods trigger the advance of a wetted front over the dry river bed. As a consequence, the alluvial section of the Albarine River is temporary, whereas the upper section of the river is perennial (Figure 1B). Two flow recorders have been measuring flow at daily intervals since January 1985 (http://www.hydro.eaufrance.fr; Figure 1B). One is 4 km upstream of the temporary section (St. Rambert en Bugey: mean river flow = 6.22 m^3/s, average annual 7-d low flow = 0.22 m^3/s), and another is in the temporary section (St. Denis en Bugey: mean river flow = 6.88 m^3/s, average annual 7-d low flow = 0 m^3/s) (Datry *et al.* 2011).

AWF and RWF

The Albarine River has a strongly seasonal drying pattern (Datry *et al.* 2011). RWFs that last several months occur in summer, whereas short RWFs that last several days occur in winter. The maximum length of the dry reach varies annually in response to runoff intensity but always is >10 km. Flow resumption in the dry reach occurs in late autumn or winter in most years. AWFs that do not cause rewetting of the entire river typically occur in response to short-duration runoff events 3 to 4 times a year. As a result, the most downstream reach of the temporary section is dry for half the year and experiences, on average, 6 to 8 AWF/y (RC and

TD, personal observation). AWFs take the form of meandering rivulets or flood bores (Figure 2A, B), depending on runoff intensity. Instantaneous velocities range from 0.1 to 1.5 m/s and velocities recorded over longer distances range from 0.05 to 0.4 km/h (RC and TD, personal observation; Figure 2A, B). We have observed several AWFs, and a video is available online (www.irstea.fr/datry).

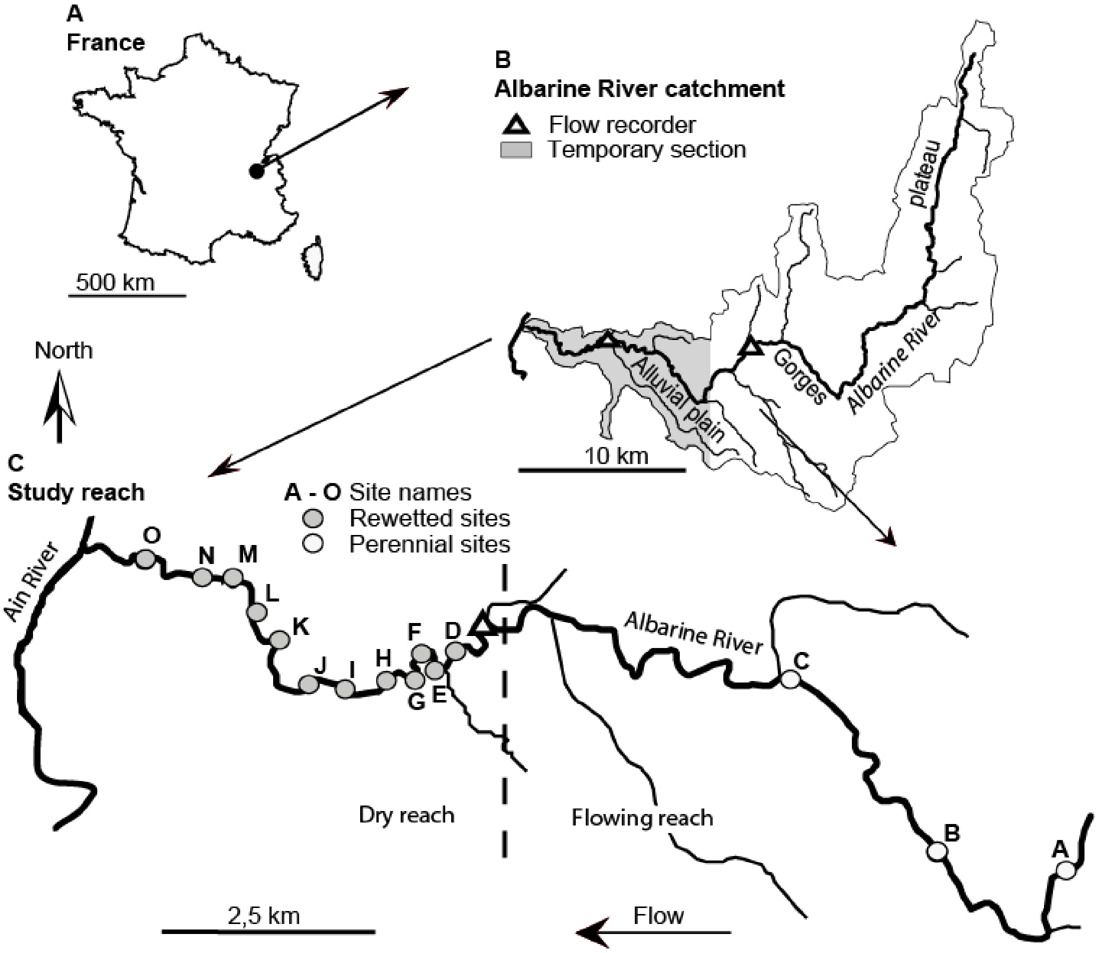

Figure 1 Maps of the Albarine River catchment (A), showing the temporary section and flow recorders (B) and the study reach in the lower area of the catchment (C). A flow event on 8 November 2010 triggered the advance of a wetted front over the dry reach from site D to the Ain River confluence.

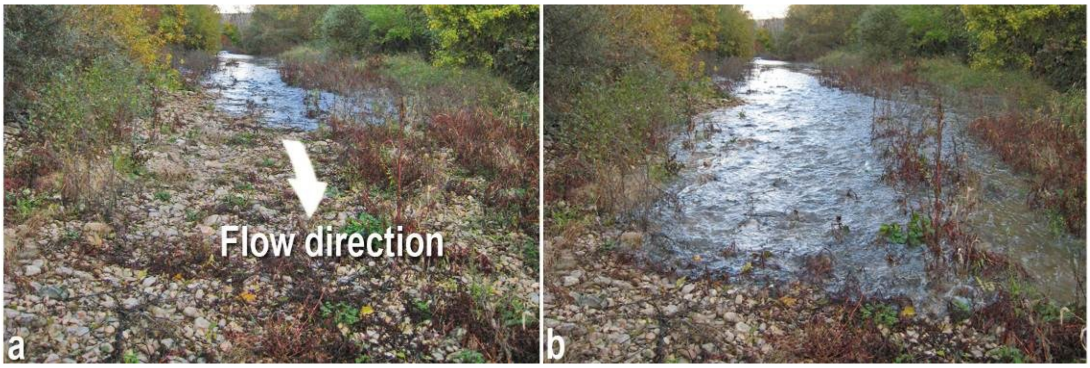

Figure 2. Upstream view of an advancing wetted front (AWF) in the Albarine River occurring on 2 November 2009. The river bed had been dry for up to 4 mo and terrestrial vegetation had grown (A). The AWF took the form of a flood bore travelling forward at a constant velocity of ~0.8 m/s (A, B). The white arrow indicates the direction of flow.

Field procedures

On 8 November 2010, as the dry reach of the Albarine River was being rewetted, we selected 3 sites that had not dried during the preceding 12 mo (perennial sites A, B, C; Figure 1C) in the flowing reach of the temporary section, 5.8 to 12.4 km upstream of the dry reach. We also selected 12 sites that had been dry for 4 to 5 mo prior to river rewetting and were 0.2 to 1.0 km apart (rewetted sites D–O; Figure 1C) along the course of the AWF. We used 1.5-m-long, 250-µm-mesh drift nets to collect 3 replicate samples of sestonic matter and 3 additional replicate samples of invertebrates sequentially at each site within 5 min of arrival of the flood bore. This technique is commonly used to sample drifting aquatic and terrestrial invertebrates in perennial rivers (Elliott 1967). However, only ¾ of the net surface was submerged so that we could collect floating organisms and organic matter (submerged net surface = 0.01 m^2) (Elliott 1967). We left nets in the stream for 100 to 160 s at perennial sites (mean ± SD = 137 ± 15 s) and from 15 to 86 s at rewetted sites (50 ± 18 s) depending on clogging by suspended sediments. We recorded water velocity at the net aperture every 5 s with a Flo-Mate 2000 velocity meter (Hach/Marsh–McBirney, Fredrick, Maryland) so that we could standardize quantities to a unit volume of water (Elliott 1967). We stored sestonic matter samples in plastic bags, transported it to the laboratory, and froze it for latter processing (see below). We separated living and dead terrestrial invertebrates in each sample immediately in the field based on visual observations. We considered an invertebrate dead if it did not move for ≥5 s and when it was picked up by forceps. We sorted only individuals >1 mm long as living terrestrial invertebrates. Individuals of this size made up 20% of terrestrial individuals and 90% of terrestrial taxa. We preserved invertebrates in 70% isopropyl alcohol prior to sorting and identification.

On 14 December 2010 (36 d after the complete rewetting of the Albarine), we collected benthic invertebrate samples from 5 sites (D, J, L, N, and O; Figure 1C). At each site, we collected 4 benthic samples at random from 2 riffle heads to minimize intrasite variability (Datry 2012). We collected invertebrates with a Hess sampler (200-µm mesh, 0.125 m^2) and preserved them in 70% isopropyl alcohol.

Laboratory procedures

We analysed sestonic matter from each sample as ash-free dry mass (AFDM). We washed sample material through 3 nested sieves (5-mm, 1-mm, and 250-µm mesh size) into a plastic box to yield 3 fractions/sample. We oven-dried (105°C, 48 h) material retained by each sieve, weighed it, combusted it in a muffle furnace (550°C, 2 h), rewetted it with distilled water, and oven-dried (105°C, 48 h) it to obtain masses at constant humidity (Wallace *et al.* 1995). We calculated organic matter content by subtracting the ash mass from the dry mass. We used sieve fractions to calculate concentrations of coarse organic and inorganic matter (>5 mm; COM and CIM, respectively), medium organic and inorganic matter (5–1 mm; MOM and MIM, respectively) and fine organic and inorganic matter (1 mm–250 µm; FOM and FIM, respectively) expressed as g/m^3.

We identified invertebrates from drift nets and benthic samples to the lowest possible taxonomic level—genus or species for most aquatic insects and Araneae, and family, class, or order for other terrestrial taxa. We considered invertebrate adults, larvae, and pupae as different taxa and classified each taxon as terrestrial, aquatic, or semiaquatic. Terrestrial invertebrates included taxa that are strict inhabitants of terrestrial habitats or are associated with shoreline environments and the surface of water (*e.g.* some Collembola and Staphylinidae). Emergent adults with aquatic larvae were classed as terrestrial if they had fully developed wings. Aquatic invertebrates included taxa that live their entire life in aquatic habitats beneath the surface of water (*e.g.* Crustacea) or were in a benthic developmental stage when collected (*e.g.* Ephemeroptera, Plecoptera, Trichoptera, and Diptera larvae). Semiaquatic taxa included those for which a definite assignment to aquatic or terrestrial classes could not be made, mainly because of the low taxonomic resolution (i.e., Acarina, Oligochaeta, and Nemathelminthes).

Data analysis

Comparison of seston concentrations and invertebrate assemblages between rewetted and perennial sites

We used Wilcoxon tests to compare sestonic matter concentrations and proportions of organic matter fraction and concentrations of organic matter fraction (COM, MOM, and FOM) between rewetted and perennial sites because data were not normally distributed (Zar 2010). We also used Wilcoxon tests to compare terrestrial, living terrestrial, aquatic, and semiaquatic taxon density and richness between rewetted and perennial sites. We used the Bray–Curtis dissimilarity index to compare terrestrial, living terrestrial, aquatic, and semiaquatic taxon assemblage composition between rewetted and perennial sites (Oksanen *et al.* 2011). We plotted patterns in dissimilarity based on nonparametric, nonmetric multidimensional scaling (NMDS) (Oksanen *et al.* 2011). We tested the significance of observed dissimilarities between rewetted and perennial sites with an analysis of similarities (ANOSIM; Clarke 1993). ANOSIM is a nonparametric procedure that evaluates whether the average similarities between samples within groups are closer than the average similarities of all pairs of replicates between groups (Clarke 1993). We did analyses on abundance data after removal of rare taxa (<0.5% of individuals). We $\sqrt{(x)}$-transformed and double standardized (Wisconsin method) composition data by dividing taxa by their maxima and then sites by their totals (Oksanen *et al.* 2011) to downweight the importance of very abundant taxa.

Longitudinal patterns

We analyzed downstream changes in COM, MOM, and FOM concentrations at rewetted sites with linear and nonlinear regressions. We also used linear and nonlinear regressions to analyze downstream changes in density and taxonomic richness of terrestrial, living terrestrial, aquatic, and semiaquatic invertebrates at rewetted sites. We tested for relationships between concentrations of organic matter fractions and total, terrestrial, living terrestrial, and aquatic invertebrate densities along the course of the AWF.

Contribution of aquatic invertebrates to benthic assemblage recovery

We examined the occurrence of each aquatic invertebrate taxon in AWF and benthic samples from the 5 sites (D, J, L, N, and O) at which both sample types had been collected. We tested downstream variation in the number of common taxa between AWF and benthic samples with linear and nonlinear regressions. We used the Bray–Curtis dissimilarity index to examine assemblage dissimilarities among AWF and benthic samples (Oksanen *et al.* 2011). Invertebrate assemblages could not be compared quantitatively because sampling techniques differed, so we calculated Bray–Curtis dissimilarity indexes on presence–absence data.

We ran all statistical analyses in R (version 2.13.0; R Development Core Team, Vienna, Austria). We used the *metaMDS* function in the *vegan* library to conduct NMDS procedures (Oksanen *et al.* 2011). We set the significance level for all statistical analyses at $p = 0.05$.

RESULTS

Characteristics of the AWF

On 8 November 2010, after a 2-d rainfall event, the AWF began to travel along the dry river bed 1-km downstream from the 2nd flow recorder (site D; Figure 1C). A flood bore developed at the leading edge of the AWF and travelled downstream at an estimated local velocity and height ranging between 0.5 and 1.0 m/s and 0.05 and 0.15 m respectively, according to channel geometry. Water depth rose rapidly after the arrival of the AWF and peaked at 0.3 m after ~10 min. One and a half days later, the AWF reached the confluence with the Ain River, 7 km downstream of the 2nd flow recorder (Figure 1C). The average AWF velocity was 0.2 km/h. Discharge registered by the 2nd flow recorder increased within 4 d from 0 to 31 m^3/s on 13 November 2010. The river reached its mean annual discharge 7 d later.

Differences between rewetted and perennial sites

Sestonic matter concentrations were on average 50× higher at rewetted sites than at perennial sites (Wilcoxon test, $p < 0.05$; median ± SD = 130.9 ± 227.4 and 4.3 ± 1.0 g/m^3 respectively). About 90% of the sestonic matter was organic, and this proportion did not differ between perennial and rewetted sites (Wilcoxon test, $p > 0.05$). The total organic matter concentration consisted primarily of COM (mean ± SD = 95 ± 9%), followed by MOM (5% ± 8%) and FOM (1 ± 1%). COM, MOM, and FOM concentrations were, on average, 60× higher at rewetted than at perennial sites (Wilcoxon tests, $p < 0.05$).

We collected 102 taxa from the drift nets, consisting of 71 terrestrial taxa (including 24 living taxa), 28 aquatic taxa, and 3 semiaquatic taxa (Table 1). The most abundant terrestrial taxa were Collembola (78% of terrestrial individuals), Psocoptera (4%), and Chrysomelidae (Coleoptera, 2%). The most abundant living terrestrial taxa belonged to 3 coleopteran families: Chrysomelidae (32% of terrestrial individuals), Staphylinidae (16%), and Carabidae (14%). The most abundant aquatic taxa were dipterans: Orthocladiinae (48%), Forcipomyiinae (12%), and Chironomidae pupae (8%). The 3 semiaquatic taxa, Oligochaeta, Acarina, and Nemathelminthes, represented 70, 28, and 2%, respectively, of semiaquatic individuals.

Table 1. List of the taxa with their abbreviations and habitat classes (T = terrestrial, A = aquatic, S = semiaquatic) collected at rewetted (R), perennial (P), and both perennial and rewetted (B) sites and their mean, minimum (min) and maximum (max) density and % occurrence (%). Density values are individuals/m^3. X indicates living terrestrial taxa.

						Density			
Taxon		Code	Habitat	Living	Sites	Mean	Min	Max	%
Nemathelminthes		Nema	S		B	6.0	0.0	44.8	35.6
Mollusca	Gastropoda	Gast	T		R	0.6	0.0	15.0	4.4
Oligochaeta		Olig	S		B	163.9	0.0	1554.4	88.9
Acarina		Aca	S		B	65.2	0.0	788.8	82.2
Araneae		Ara	T		R	6.6	0.0	60.0	40.0
	Alopecosa sp.	Alo	T	X	R	0.1	0.0	2.6	2.2
	Araneidae	Arad	T	X	R	0.2	0.0	6.9	4.4
	Mangora acalypha	Man	T		R	1.3	0.0	15.0	17.8
	Ballus sp.	Ball	T		R	0.2	0.0	7.1	2.2
	Clubiona sp.	Clu	T		R	0.7	0.0	21.3	8.9
	Drassodes sp.	Dra	T	X	R	0.2	0.0	7.5	2.2
	Haplodrassus sp.	Haplo	T	X	R	0.2	0.0	9.2	2.2
	Linyphiidae a	Lyna	T		R	1.5	0.0	12.0	17.8
	Linyphiidae b	Lynb	T	X	B	8.3	0.0	85.9	51.1
	Lepthyphantes tenuis	Lept	T		R	0.6	0.0	12.9	6.7
	Micaria sp.	Mic	T		R	0.1	0.0	2.3	2.2
	Oxyopes sp.	Oxyo	T		P	0.0	0.0	0.9	2.2
	Pardosa sp.	Pard	T	X	R	1.1	0.0	14.9	11.1
	Pirata sp.	Pir	T		R	0.3	0.0	11.5	4.4
	Pisaura sp.	Pis	T		R	0.4	0.0	15.0	4.4
	Tegenaria sp.	Tege	T		R	0.2	0.0	5.6	4.4
	Tetragnatha sp.	Tetra	T	X	B	0.1	0.0	2.3	6.7
	Therididae	Therid	T	X	R	1.5	0.0	21.3	17.8
	Episinus sp.	Epi	T		R	0.8	0.0	16.6	11.1
	Theridion sp.	Ther	T		B	1.2	0.0	25.8	20.0
	Thomisidae	Thom	T		R	0.3	0.0	11.9	2.2
	Ozyptila sp.	Ozyp	T		R	0.1	0.0	3.5	2.2
	Zelotes sp.	Zel	T		R	0.1	0.0	2.7	2.2
	Zora sp.	Zora	T		R	0.6	0.0	21.3	4.4
Opiliones		Opi	T		R	0.2	0.0	7.6	2.2
Crustacea	Cladocera	Clad	A		B	2.3	0.0	59.7	15.6
	Cyclopoida	Cycl	A		B	0.2	0.0	3.6	6.7
	Oniscidea	Onis	T	X	R	7.6	0.0	43.4	40.0
	Ostracoda	Ostr	A		B	0.9	0.0	16.3	8.9
Myriapoda	Chilopoda	Chil	T		R	0.9	0.0	19.0	13.3
	Diplopoda	Diplo	T		R	1.3	0.0	19.0	15.6
Collembola		Col	T	X	B	1328.0	0.0	17495.5	93.3
Coleoptera	Adult	Col3	T	X	R	31.0	0.0	165.0	75.6
	Larva	Col1	T	X	R	6.6	0.0	60.0	37.8
	Carabidae	Cara	T	X	R	8.5	0.0	47.8	62.2
	Chrysomelidae	Chrys	T	X	B	40.3	0.0	167.2	77.8
	Coccinellidae	Cocc	T		R	0.3	0.0	15.0	2.2
	Curculionidae	Curc	T		R	0.3	0.0	12.6	4.4
	Esolus sp. (adult)	Esol3	A		B	0.6	0.0	9.5	11.1
	Esolus sp. (larva)	Esol1	A		P	0.0	0.0	1.0	2.2
	Hydrophilidae	Hydr	A		R	0.2	0.0	7.1	2.2
	Limnius sp. (adult)	Limn3	A		P	0.0	0.0	0.9	2.2
	Oulimnius sp. (adult)	Oulimn3	A		R	0.2	0.0	6.9	4.4

Taxon		Code	Habitat	Living	Sites	Density			%
	Ptiliidae	Pti	T		R	1.5	0.0	13.6	22.2
	Staphylinidae	Sta	T	X	B	37.2	0.0	206.5	84.4
Dermaptera		Derm	T	X	R	0.1	0.0	2.6	2.2
Diptera	Diptera (adult)	Dipt3	T	X	B	27.0	0.0	107.9	82.2
	Diptera (larva)	Dipt1	T	X	R	14.1	0.0	71.7	66.7
	Diptera (pupa)	Dipt2	T	X	B	2.4	0.0	38.1	17.8
	Cecidomyiidae	Ceci	T		B	9.1	0.0	68.8	48.9
	Ceratopogoninae	Cera	A		R	0.5	0.0	11.9	6.7
	Chaoborus sp.	Chao	A		R	0.1	0.0	4.0	2.2
	Chironomidae (adult)	Chiro3	T		B	25.2	0.0	171.4	82.2
	Chironomidae (larva)	Chiro1	A		P	0.0	0.0	1.0	4.4
	Chironomidae (pupa)	Chiro2	A		B	2.6	0.0	38.1	37.8
	Chironominae	Chiron	A		B	0.5	0.0	9.5	15.6
	Dasyheleinae	Dasy	A		R	1.8	0.0	81.0	2.2
	Faniidae	Fani	T		R	1.1	0.0	28.6	8.9
	Forcipomyiinae	Forci	A		R	3.8	0.0	68.8	17.8
	Hemerodromiinae	Hem	A		P	0.0	0.0	1.0	2.2
	Lonchopteridae	Lon	T		B	1.0	0.0	11.5	17.8
	Orthocladiinae	Orth	A		B	15.7	0.0	171.9	53.3
	Psychodidae (larva)	Psyc1	A		B	0.7	0.0	15.0	8.9
	Psychodidae (pupa)	Psyc2	A		R	1.8	0.0	38.0	13.3
	Scatopsidae	Sca	T		R	2.0	0.0	38.2	15.6
	Stratiomyidae	Stra	A		B	0.2	0.0	5.4	4.4
	Syrphidae	Syr	T	X	R	0.4	0.0	11.9	4.4
	Tanypodinae	Tany	A		P	0.1	0.0	1.8	4.4
Ephemeroptera	Baetidae (Pupa)	Bae	A		P	0.0	0.0	1.8	2.2
	Centroptilum luteolum	Cen	A		B	0.1	0.0	3.6	4.4
	Caenis sp.	Cae	A		P	0.0	0.0	1.0	2.2
Hemiptera	Adult	Auch3	T		R	0.6	0.0	7.8	11.1
	Auchenorrhyncha	Auch1	T		B	4.0	0.0	57.3	22.2
	Cicadellidae	Cyca	T	X	R	3.6	0.0	23.9	37.8
	Heteroptera (adult)	Hete3	T	X	B	9.0	0.0	45.0	53.3
	Heteroptera (larva)	Hete1	T		R	0.5	0.0	7.6	6.7
	Pyrrhocoris sp.	Pyrr	T		R	0.2	0.0	7.0	2.2
	Sternorrhyncha (larva)	ster1	T		B	1.5	0.0	15.2	17.8
	Aleyrodidae	Aley	T		R	1.0	0.0	19.3	11.1
	Aphididae	Aphi	T		B	15.0	0.0	90.1	68.9
	Psyllidae	Psy	T		B	4.9	0.0	32.6	40.0
Hymenoptera		Hym3	T		R	4.1	0.0	38.6	40.0
	Apocrita	Apo	T	X	B	12.7	0.0	44.0	66.7
	Cynipidae	Cyn	T		R	2.3	0.0	33.1	15.6
	Formicidae	Form	T	X	B	1.7	0.0	20.0	20.0
	Myrmicinae	Myrm	T		R	0.1	0.0	2.3	2.2
	Symphyta	Sym	T		R	1.9	0.0	12.6	24.4
Lepidoptera		Lepi	T		R	3.4	0.0	30.0	28.9
Neuroptera		Neur	T		R	0.4	0.0	6.4	6.7
Plecoptera	Adult	Plec	T		R	0.1	0.0	3.5	2.2
	Leuctra sp.	Leu	A		P	0.0	0.0	1.3	4.4
Psocoptera		Pso	T		B	68.1	0.0	379.9	82.2
Thysanoptera		Thys	T		B	3.7	0.0	23.9	42.2
Trichoptera	Adult	Tric3	T		B	0.2	0.0	7.6	4.4
	Limnephilidae	Limn	A		R	0.2	0.0	6.9	2.2
	Mystacides sp.	Mysr	A		P	0.0	0.0	0.9	2.2
	Rhyacophilidae	Rhya	A		P	0.0	0.0	1.8	2.2

The AWF assemblage was dominated by terrestrial individuals (81 ± 17%), with some semiaquatic individuals (17 ± 16%) and aquatic individuals (2 ± 3.5%). In contrast, invertebrate composition at perennial sites was a combination of terrestrial and aquatic individuals 54 ± 25.8% and 36 ± 18.4%, respectively) and a few semiaquatic individuals (10 ± 9.1%). Terrestrial invertebrate density was on average 200× higher and taxonomic richness 5× higher at rewetted than at perennial sites (Wilcoxon test, $p < 0.001$; median ± SD = 1092 ± 3346 and 11 ± 7 individuals ind/m^3, respectively; Figure 3A). In addition, we found 48 terrestrial taxa only at rewetted sites, 1 only at perennial sites (*Oxyopes* sp., Araneae), and 22 at rewetted and perennial sites (Table 1). On average, 38 ± 32 ind/m^3 were still alive in drift nets at rewetted sites, whereas no living terrestrial taxon was collected at perennial sites. Aquatic invertebrate density was 6× higher but taxonomic richness 2× lower at rewetted than at perennial sites (Wilcoxon test, $p < 0.001$ for all tests; 24 ± 39 and 6 ± 4 ind/m^3, respectively; Figure 3B). Eight aquatic taxa were found only at rewetted sites, whereas 10 were found only at perennial sites and 10 were found at rewetted and perennial sites (Table 1). Density of semiaquatic invertebrates was, on average, 160× higher and taxonomic richness 2× lower at rewetted than at perennial sites (Wilcoxon test, $p < 0.001$ for all tests; 133 ± 418 and 1 ± 2 ind/m^3, respectively) (Figure 3C). Semiaquatic taxa (Acarina, Oligochaeta, and Nemathelminthes) were found at both rewetted and perennial sites (Table 1).

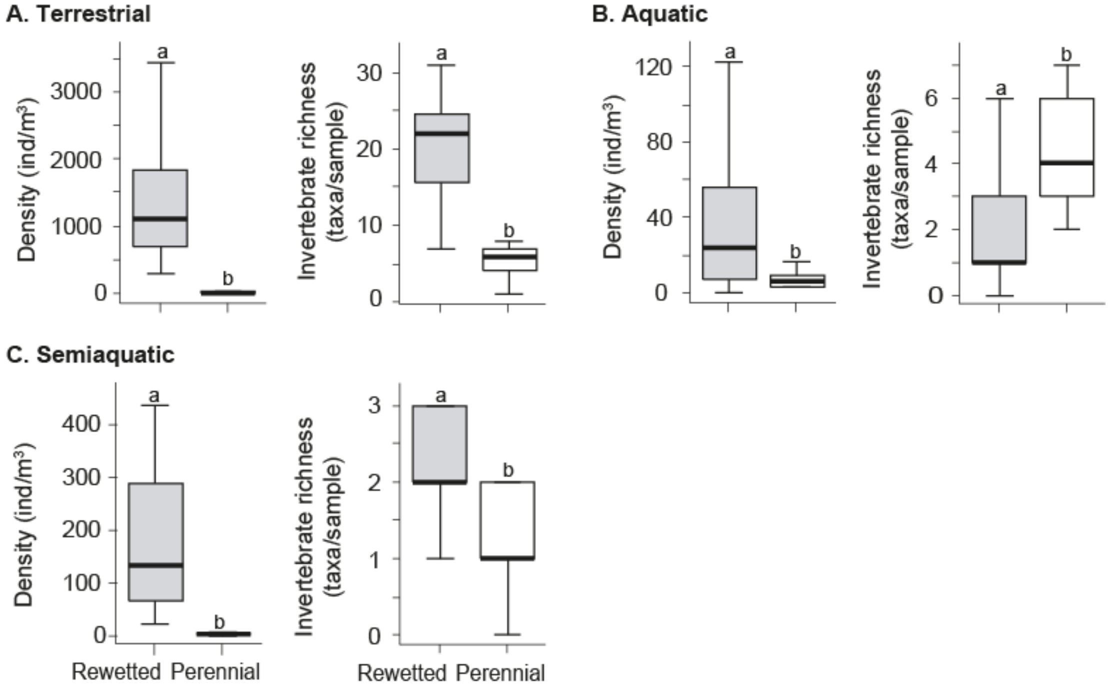

Figure 3 Density and taxonomic richness of terrestrial (A), aquatic (B), and semiaquatic (C) invertebrates entrained at rewetted and perennial sites. Box plots show the median (solid line),

25th and 75th percentiles (box ends), and 10th and 90th percentiles (whiskers). Different lower-case letters indicate statistical significant differences based on Wilcoxon tests.

The composition of terrestrial assemblages differed significantly between rewetted and perennial sites (NMDS stress value < 0.001, 1-way ANOSIM, global $R = 1$, $p = 0.001$; Figure 4A). Rewetted sites were associated with higher densities of 67 terrestrial taxa, whereas perennial sites were associated with higher densities of 1 Trichoptera adult and 2 Araneae taxa (*Tetragnatha* sp. and *Oxyopes* sp.). No living terrestrial taxon was recorded at perennial sites (Figure 4B). Aquatic assemblage composition did not differ between rewetted and perennial sites (NMDS stress value = 0.14, 1-way ANOSIM, global $R = 0.30$, $p = 0.08$; Figure 4C). Composition of semiaquatic taxon assemblages differed considerably between rewetted and perennial sites. Rewetted sites had higher densities of Acarina, Nemathelminthes, and Oligochaeta (NMDS stress value < 0.001, 1-way ANOSIM, global $R = 0.97$, $p = 0.004$; Figure 4D).

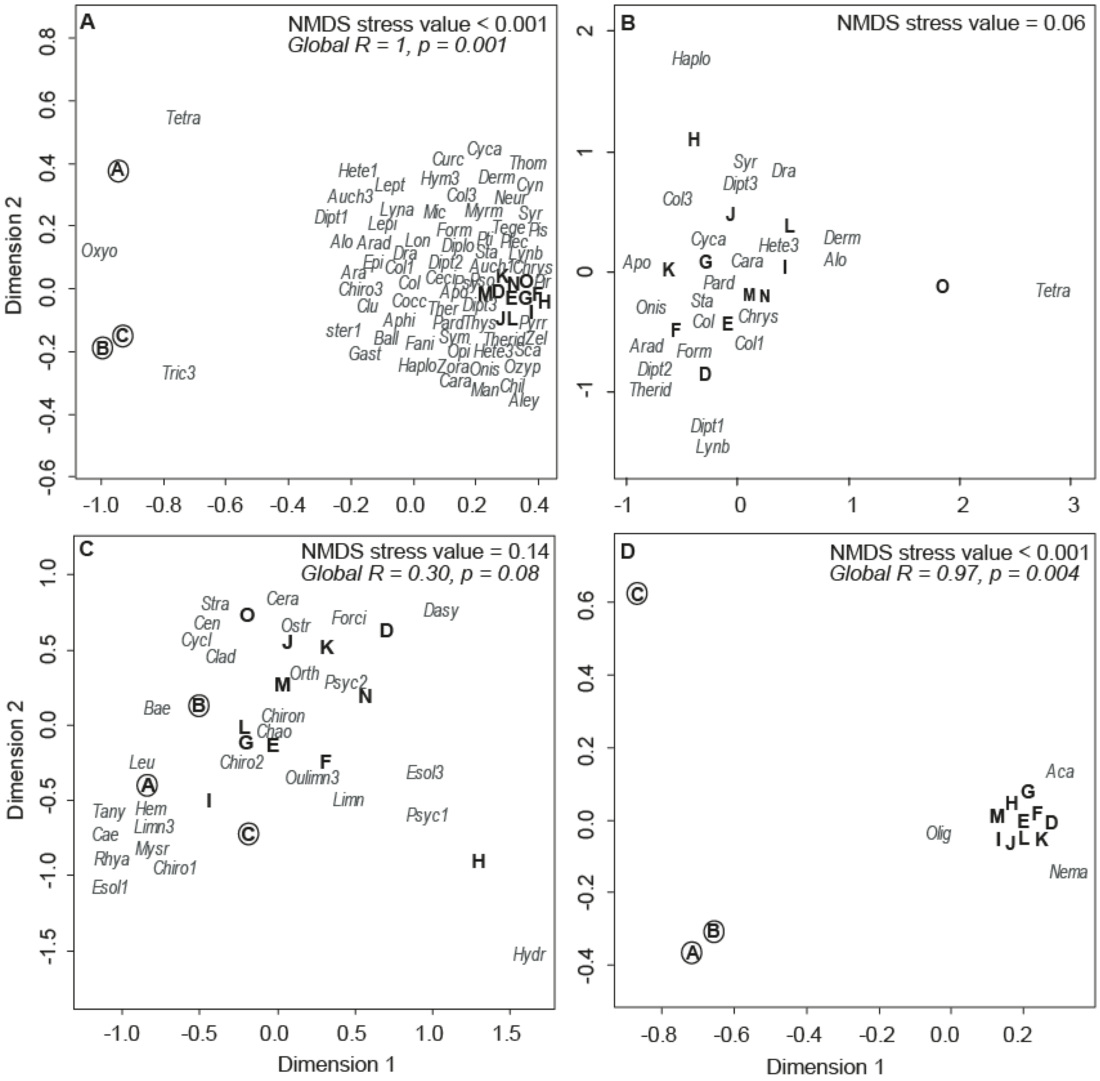

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination of terrestrial (A), living terrestrial (B), aquatic (C), and semiaquatic (D) invertebrate assemblages collected at rewetted and perennial sites. See Table 1 for taxon codes and Figure 1 for site codes (capital letters). Open circles indicate perennial sites. Note the absence of living terrestrial taxa in perennial sites on plot B.

Longitudinal variations in seston and invertebrate assemblages

COM, MOM, and FOM concentrations were not related to distance downstream ($R^2 < 0.2$, $p > 0.05$ for all tests; Figure 5A–C). Terrestrial invertebrate density also was not related to distance downstream ($R^2 = 0.1$, $p > 0.05$). In contrast, terrestrial taxonomic richness increased linearly with distance downstream ($R^2 = 0.34$, $p < 0.05$; Figure 6A). On average, 2 terrestrial taxa were added to the AWF for every 1 km travelled downstream. Density of living terrestrial invertebrates decreased exponentially with distance downstream, whereas their taxonomic richness decreased linearly ($R^2 = 0.52$ and $R^2 = 0.37$, respectively, $p < 0.05$; Figure 6B). Densities of living terrestrial invertebrates decreased by ½ in the first 3 km, and on average, 1 living taxon disappeared from the AWF for every 1 km travelled downstream. Neither aquatic invertebrate density nor taxonomic richness was related to distance downstream ($R^2 = 0.1$ and 0.12 respectively, $p > 0.05$ for all tests; Figure 6C). Semiaquatic invertebrate density was not related to distance downstream ($R^2 = 0.1$, $p > 0.05$), whereas their taxonomic richness increased linearly with distance downstream ($R^2 = 0.50$, $p = 0.02$; Figure 6D). COM, MOM, and FOM were not significantly related to terrestrial, living terrestrial, aquatic, or semiaquatic taxon density and richness ($R^2 < 0.2$, $p > 0.05$ for all tests).

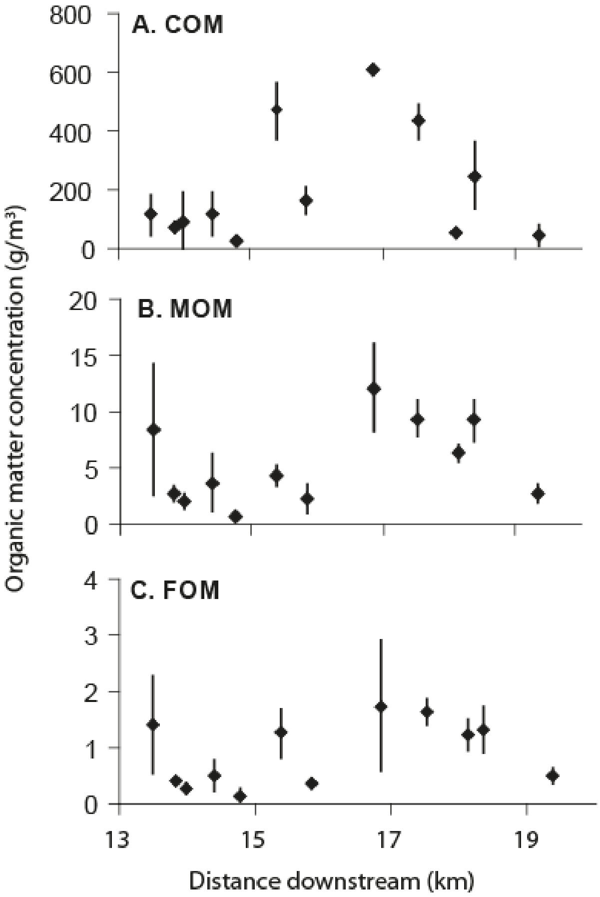

Figure 5 Mean (±1 SD) concentrations of coarse organic matter (COM) (A), medium organic matter (MOM) (B), and fine organic matter (FOM) (C) entrained during the advance of the wetted front.

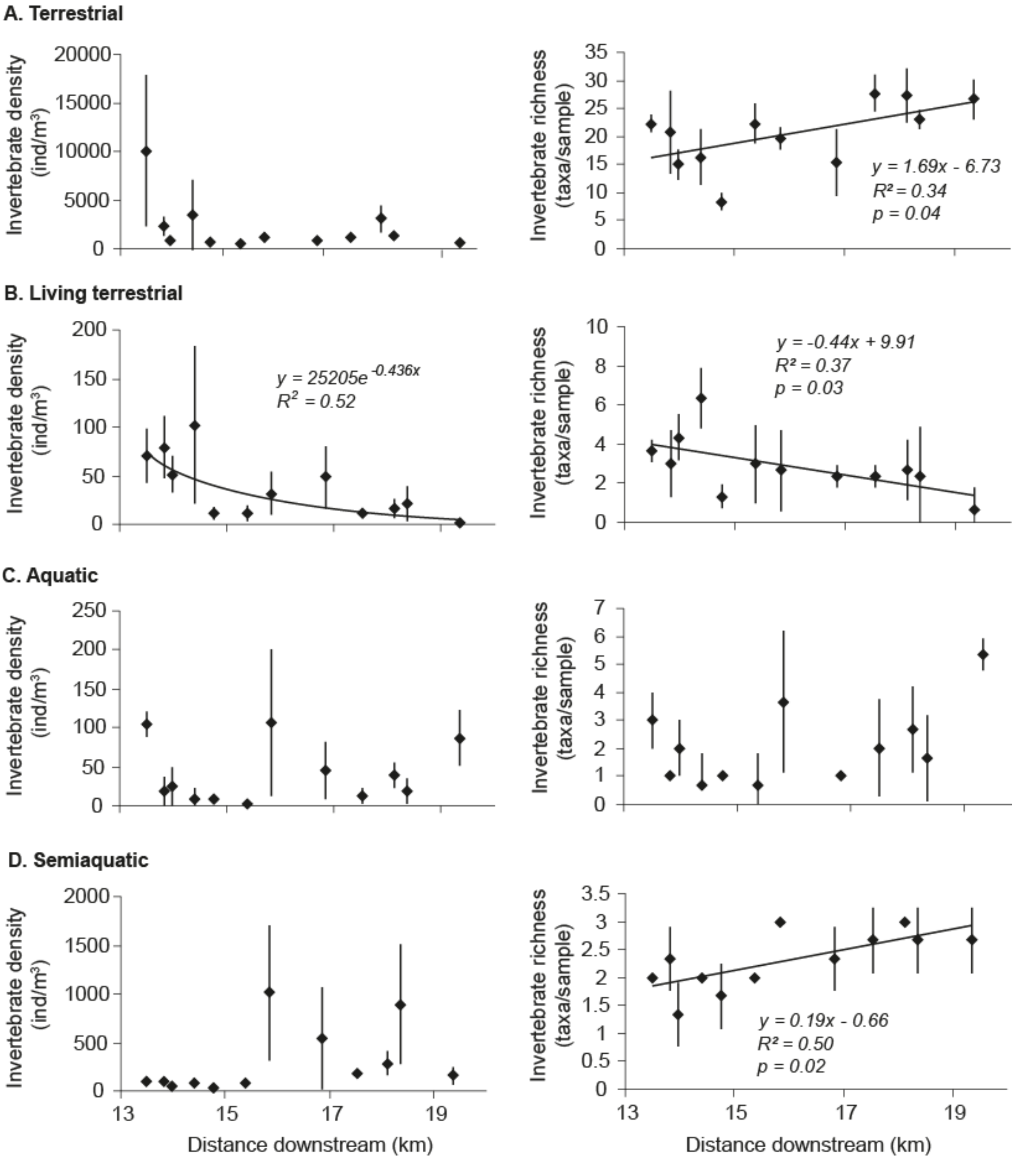

Figure 6 Mean (±1 SD; n = 3) density and taxonomic richness of terrestrial (A), living terrestrial (B), aquatic (C), and semiaquatic (D) invertebrates entrained during the advance of the wetted front. Regression curves are shown for significant longitudinal relationships.

Contribution of aquatic invertebrates to benthic assemblage recovery

A total of 29 aquatic taxa were found in benthic assemblages 36 d after complete rewetting, whereas 11 aquatic taxa had been found in the AWF at the same sites. AWF and benthic assemblages had only 5 taxa in common (4 Diptera and 1 Ostracoda), indicating that the number of taxa present in the AWF represented only 14% of the number of taxa present in benthic assemblages. The average number of taxa common to both sample types was 2.2 ± 1.3 taxa ($n = 5$) and did not vary with distance from perennial sites nor distance downstream ($R^2 = 0.2$, $p > 0.05$ for both tests). The Bray–Curtis dissimilarity index calculated on presence–absence data indicated that after rewetting, AWF and benthic assemblages were weakly similar in composition (24 ± 8%).

DISCUSSION

Longitudinal pulses in invertebrates and sestonic matter

The AWF contained very large quantities of invertebrates and sestonic matter that were flushed from the dry river bed and exported downstream during the flood. The density of invertebrates was several orders of magnitude greater in the AWF along the rewetted reach than in the perennial reach of the Albarine or compared to values reported from other perennial rivers during peak flows (Rincon and Lobon-Cervia 1997, Tockner and Waringer 1997, Romaniszyn *et al.* 2007). Sestonic matter concentrations in the AWF were, on average, 500× higher than concentrations reported from perennial rivers during the leaf-abscission period (Bilby and Bisson 1992, Wallace *et al.* 1995). These large quantities were the result of accumulation of poorly decomposed leaves on dry riverbed sediments (Corti *et al.* 2011, Dieter *et al.* 2011) and colonization of the dry river bed by terrestrial invertebrates (Wishart 2000, Steward *et al.* 2011) during the 4-mo dry period before river rewetting. These quantities could be lower in the short AWFs that occur, on average, 3 to 4× during spring and summer. However, they are likely to be much greater after longer dry periods when river rewetting occurs later in the year at the end of the leaf-abscission period.

The input of large amounts of terrestrially derived materials to newly created aquatic habitats constitutes a longitudinal pulse analogous to lateral flood pulses observed in large perennial rivers (Junk *et al.* 1989, Tockner *et al.* 2000). AWFs deliver different types of organic matter to downstream aquatic habitats, including dried biofilms, dead and living invertebrates, leaves, and wood. Dissolution of sediment evaporites and leaching of accumulated organic matter also may cause associated spikes in solute and nutrient concentrations during the flood (Jacobson *et al.* 2000, Bernal *et al.* 2002, Obermann *et al.* 2009). This pulse may stimulate aquatic productivity of downstream reaches by providing electron donors to microbial communities and sources of food for consumers, thereby resulting in bursts of autochthonous production. Predatory and detritivorous fishes could migrate from perennial refuges to rewetted reaches to exploit these temporary inputs of terrestrial invertebrate prey and organic matter, as has been observed in river floodplains during expansion phases (Eberle and Stanford 2010). Alternatively, these substantial fluxes of organic material also could have negative consequences for downstream reaches and receiving ecosystems (*e.g.* confluences, reservoirs, estuaries) via development of hypoxic conditions (Townsend and Edwards 2003) or the colmation of riverbed sediments (Argerich *et al.* 2011).

Invertebrates and sestonic matter did not accumulate longitudinally in the AWF, and this result suggests the existence of intermediate zones of deposition and accumulation. Neither terrestrial invertebrate density nor sestonic matter concentration increased with distance downstream, and the composition of invertebrate assemblages did not change longitudinally. Rather, we found important between-site variations along the course of the AWF. No confluences with tributaries occur along this reach, so these differences indicate that most terrestrial invertebrates and sestonic matter were entrained for only short distances (<2 km) and redeposited as the AWF progressed downstream. Storage zones may develop near structures formed by flow obstructions, such as scour pools, bar tops, and tight bends (Buffington *et al.* 2002, Jacobson and Jacobson 2012). Overall, trade-offs between mobilization and storage of organic material along the rewetted reach may control the quantities exported to the downstream confluence with the Ain River.

A dispersal pathway for terrestrial invertebrates

The AWF was a catastrophic event for many terrestrial taxa, but some taxa might use it as a dispersal pathway to colonize downstream riparian areas. In total, ⅓ of terrestrial taxa collected from the AWF were found alive, and their density decreased with distance downstream. These taxa are likely to display behavioral, morphological, or life-history adaptations that enable them to avoid death by: 1) abandoning the river bed before a flood arrives (Lytle and White 2007, Lambeets *et al.* 2008); 2) floating, swimming, or climbing onto organic matter; or 3) respiring through air bubbles (Boumezzough and Musso 1983). Regardless of which strategy they use, their ability to survive riverbed rewetting may depend on the form and velocity of AWFs. Rapid flood bores are expected to entrain more taxa than bores from expanding pools of upwelling groundwater, which are generally much slower (Doering *et al.* 2007). In the Albarine River, storage zones might have allowed living invertebrates (*e.g.* Chrysomelidae, Staphylinidae, Carabidae, and Lycosidae) to move toward adjacent riparian-zone and more-elevated upland habitats. Therefore, the longitudinal distribution of these structures may create hotspots of terrestrial biodiversity adjacent to the river. In turn, these hotspots could be sources of colonists for colonization of the river bed during subsequent dry periods.

Terrestrial assemblages along the dry Albarine River probably were structured longitudinally prior to rewetting. Terrestrial taxonomic richness increased, whereas taxonomic richness of living terrestrial taxa decreased longitudinally in the AWF, a result suggesting a longitudinal shift in dry riverbed assemblage composition. Changes in environmental conditions along the dry river bed, notably associated with the increasing duration of the dry period with distance downstream, may partly explain these shifts. For example, sediment moisture decreases with distance downstream in the Albarine River (Datry 2012), whereas the density of annual herbs is likely to increase (Werger 1978). Sediment moisture is a strong driver of terrestrial biodiversity (Antvogel and Bonn 2001) and many invertebrates, such as Chrysomelidae, Cucurlionidae, Homoptera, and Formicidae, use nectar, fruits, leaves, and seeds of plants as food sources (Hölldobler and Wilson 1990, Jolivet and Hawkeswood 1995). Longitudinal structure of aquatic invertebrate assemblages is widely reported in temporary rivers (Datry *et al.* 2007, Arscott *et al.* 2010, Datry 2012) and may also occur for terrestrial invertebrate assemblages, although the ecology of dry river beds is still poorly understood (Steward *et al.* 2012).

Rewetting and aquatic invertebrates

The AWF transported from upstream perennial reaches a subset of aquatic invertebrates that could colonize newly created benthic habitats. The most abundant aquatic taxa entrained by the flow were Diptera (Orthocladiinae, Forcipomyiinae, and other Chironomidae) and Crustacea (Cladocera and Ostracoda). Together with the Oligochaeta, these taxa are typically associated with pools, ponds, and other lentic habitats, in which annual invertebrate production can be 1 to 2 orders of magnitude greater than production in the stream channel (Gladden and Smock 1990). Concentration of these taxa in receding pools in areas where the river was drying could explain the high aquatic and semiaquatic densities found in the AWF along the rewetting reach (Stanley *et al.* 1994, Acuña *et al.* 2005). These taxa exhibit traits of r-selected species, including high dispersal capacity, rapid growth, and short life span (Williams 1996). However, the density and taxonomic richness of aquatic invertebrates were not related to the distance from the upstream perennial reach and varied considerably along the course of the AWF, indicating that the dispersal of aquatic invertebrates by the AWF may be predominantly passive. Like terrestrial invertebrates and sestonic matter, drifting aquatic taxa are likely to be deposited and recruited in storage zones. Recruitment of pioneer aquatic invertebrates may contribute to the rapid recovery of aquatic assemblages generally observed in temporary rivers upon rewetting (Stanley *et al.* 1994, Churchel and Batzer 2006).

Very few of the taxa entrained by the AWF were found in the benthos 1 mo after rewetting, a result suggesting these assemblages were not at the same successional stage. After pioneer taxa from the AWF settled to the river bed, additional sources of colonists might have contributed to community succession via recruitment of new species and exclusion of poorly competitive ones (Boulton and Lake 1992). Hyporheic sediments were probably a poor source of colonists in the Albarine River because they typically dry completely within 5 to 15 d of surface drying (Datry 2012). Aquatic drift from perennial refuges after initial riverbed rewetting and subsequent oviposition by aerial adults may be important sources of colonists (Paltridge *et al.* 1997), but their relative contributions to community development have not been quantified in the Albarine River. Last, nearly ½ of the benthic taxa present before and after dry periods may persist in dry riverbed sediments as desiccation-resistant forms (Datry *et al.* 2012). Such taxa may make a substantial contribution to aquatic succession in the Albarine River after rewetting. The existence of individual or combined sources of colonists is likely to be related to spatial patterns of drying across river networks (*e.g.* upstream, mid-reach, downstream, and complete drying; Lake 2003). Therefore, the distribution of perennial refuges within river networks may be a major factor controlling the distribution and the organization of aquatic assemblages in temporary rivers.

Conclusions

Temporary rivers make up a large part of the flowing water across the planet and will increase in the future because of increasing pressure on water resources (Larned *et al.* 2010, Döll and Müller Schmied 2012). Global change and consequent water stress may also move forward the timing of leaf abscission, which is likely to increase the quantity of leaves accumulated in dry river beds (Acuña *et al.* 2007). However, models of organic matter processing and aquatic community organization in rivers (*e.g.* nutrient spiraling concept, Webster and Patten 1979; river continuum concept, Vannote *et al.* 1980, network dynamic hypothesis, Benda *et al.*

2004) do not account for dry phases and transitional periods from dry to wet conditions. Our study adds evidence to others (*e.g.* Larned *et al.* 2010, Corti *et al.* 2011) that current conceptual and empirical models in river ecology necessitate to be extended to include temporary rivers and dry periods.

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7

TRANSITIONS TERRESTRE-AQUATIQUE ET DECOMPOSITION DE LA MATIERE ORGANIQUE

Article 5

Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river.

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ABSTRACT

Flow pulses that alternately immerse and expose benthic habitats are widely recognized as key determinants of biodiversity and ecosystem functioning in rivers. Terrestrial leaf litter input, colonization, and breakdown are also key processes in river ecosystems, but little is known about the effects of alternating immersion and emersion on these processes. We used litterbags to examine breakdown, microbial activity, and colonization of *Populus* sp. leaves by invertebrates along a natural gradient in immersion and emersion (i.e., submergence and exposure to air) in a temporary river. Rates of leaf litter mass loss, microbial activity and colonization by invertebrates differed among litterbags that were permanently immersed, intermittently immersed and permanently emersed, and breakdown rate coefficients (k) decreased with increasing cumulative emersed duration (the total number of day of emersion during the experiment). In contrast, the frequency of emersed periods had no detectable effects on these variables. k was positively correlated with the density of invertebrate shredders in immersed litterbags, with microbial activity and shredder density in intermittent litterbags, and with microbial activity in emersed litterbags. These correlations suggest that the relative importance of microbial activity on k increases with emersed duration, due to the periodic elimination of aquatic shredders and the scarcity of terrestrial detritivores. The fact that leaf litter breakdown was detectable under permanently emersed conditions indicates that mechanisms other than shredding by invertebrates, such as leaching and photodegradation, are dominant in dry river habitats.

Key-words: terrestrial leaf litter, immersion-emersion cycles, terrestrial and aquatic invertebrates, microbial activity, scour pool

INTRODUCTION

Hydrologic variability is a key determinant of community diversity and ecosystem processes in river-floodplain systems. Daily or weekly flow pulses that remain below bank-full drive expansion-contraction cycles in many alluvial rivers (*e.g.* Stanley *et al.* 1997; Tockner *et al.* 2000). In turn, expansion and contraction of wetted areas cause benthic habitats to be alternately immersed in water and exposed to air (emersed). Alternating immersion and emersion increases habitat heterogeneity and affects biodiversity and biogeochemical processes (Tockner *et al.* 2000; Langhans and Tockner 2006; Datry and Larned 2008).

Terrestrial leaf litter input and breakdown and colonization of leaf litter by invertebrates are critical ecosystem processes in many rivers. The composition and lability of litter, rates and timing of litter input, and litter breakdown rates all influence river food web structure, nutrient cycling, heterotrophic energy flow, and habitat availability (Petersen and Cummins 1974; Wallace *et al.* 1997; Webster *et al.* 2001). Under immersed conditions, leaf litter is colonized by benthic macroinvertebrates within days; measured litterbags colonization rates over a month range from 1 to 80 individuals g^{-1} litter day^{-1} (Petersen and Cummins 1974; Langhans *et al.* 2008; Gaudes *et al.* 2009; Ligeiro *et al.* 2010). Results from experiments with natural and artificial leaves suggest that the primary value of leaf litter for macroinvertebrates is as a food source, and its value as habitat is secondary (Richardson 1992). Colonization of immersed leaf litter by macroinvertebrates is selective, and aquatic leaf-shredding invertebrates preferentially feed on leaves that have been conditioned by micro-organisms (Chergui and Pattee 1991; Abelho 2008). Shredding invertebrates have a major role in litter breakdown in some, but not all rivers (Rounick and Winterbourn 1983; Gonçalves *et al.* 2007). In rivers with low densities of leaf-shredding macroinvertebrates, bacteria, fungi and protozoans dominate the biotic stages of litter breakdown (Benstead *et al.* 2009; Tank *et al.* 2010).

Temporary rivers are among the most hydrologically dynamic freshwater ecosystems (Larned *et al.* 2010a). The repeated onset and cessation of flow causes temporary rivers to contract and expand in the lateral and longitudinal dimensions, alternately immersing and exposing channel sediments. Temporary rivers are very common, but the state of knowledge concerning organic matter dynamic in these rivers is poor (Larned *et al.* 2010a; Datry *et al.* 2011). This knowledge gap limits our understanding of the range of pathways that exist for allochthonous organic matter processing in rivers. There is evidence suggesting that emersion inhibits colonization of leaf litter by aquatic leaf-shredding invertebrates, and that immersion duration and frequency influence litter breakdown in temporary river habitats (Boulton 1991; Langhans and Tockner 2006; Datry *et al.* 2011). The effects of emersion on micro-organisms colonizing leaf litter and on microbial decomposition are less clear. Results of some studies indicate that alternating emersion and immersion stimulates micro-organism colonization and activity (Swift *et al.* 1979; Ryder and Horwitz 1995). Results of other studies suggest that the primary effect of emersion is to reduce microbial activity (Boulton 1991; Datry *et al.* 2011). Microbial decomposition clearly occurs during emersed periods, particularly when the litter is partially rehydrated by high humidity, rainfall or dew (Kuehn *et al.* 2004; Langhans and Tockner 2006). Solar photochemical mineralization may also contribute to leaf litter decomposition during emersed periods (Austin and Vivanco 2006). Finally, diverse terrestrial invertebrate assemblages, including leaf shredders, inhabit riparian zones (Uetz *et al.* 1979; Hutchens and Wallace 2002; Paetzold *et al.* 2008; Greenwood and McIntosh 2008), and some of these shredders may move into river channels and process litter during emersed periods.

In the present study, we measured leaf litter breakdown (as mass loss), microbial activity on leaf litter, and colonization of leaf litter by aquatic and terrestrial invertebrates along a natural gradient of immersion and emersion. We used scour pools in a perennial and an ephemeral section of an alluvial river as experimental units; water-depth fluctuations in these pools generated the immersion-emersion gradient. Scour pools are common morphological features in alluvial rivers, particularly at sites of convergent flow, and sites where flow obstructions cause large turbulent eddies (Reinfields and Nanson 1993; Buffington *et al.* 2002). The high density of scour pools in our study area (> 10 pools km^{-1}) provided a natural experimental system for identifying effects of immersion-emersion cycles on the fate of leaf litter and on invertebrate colonization patterns. On the basis of the preceding observations, we made three predictions. First, leaf-litter breakdown would be inversely related to both the frequency and duration of emersed periods, due to the negative effects of drying on litter processing by aquatic invertebrates and microbes. Second, aquatic shredder colonization and subsequent effects on litter breakdown would be inversely related to both emersion frequency and the cumulative duration of emersion. As a corollary, we predicted that the relative importance of microbial decomposition compared with invertebrate shredding would increase directly with emersion frequency and cumulative emersed duration. Our third prediction was that microbes and terrestrial shredders would colonize and process leaf litter in riverine habitats during emersed periods.

METHODS

Study location

The Selwyn River rises in the foothills of New Zealand's Southern Alps, and flows east through the foothills and across the Canterbury Plains to Lake Ellesmere, on the east coast of the South Island (Figure 1a, b). The upper (western) Canterbury Plains in the vicinity of our study area are composed of Pleistocene glacial and periglacial outwash, post-glacial alluvium, and thin, loess-dominated soils (Taylor *et al.* 1989). Alluvial aquifers in the upper plains are poorly-confined and overlain by a 15-50 m thick vadose zone. The Selwyn River is perched above the vadose zone in this region, and surface water seeps downward from the river channel through the vadose gravels, to the underlying aquifer. Rapid seepage leads to progressive flow loss with distance down the Selwyn River channel, and all flow is lost for part of most years beginning ~ 3 km downstream of the foothills-plains border (Larned *et al.* 2008). This point separates an upstream perennial section of the river from a downstream ephemeral section. In the ephemeral section, the length of dry channel varies in response to runoff from the foothills. Flow extends down the entire 38-km ephemeral section only during long periods of high runoff, and the entire section is dry during long periods of low runoff. Higher frequency flow expansion and contraction occurs in response to short-lived runoff events (Larned *et al.* 2010b). The 3-km long reach used in the current study included the downstream-most portion (1-km long) of the perennial section, and the upstream-most portion (2-km long) of the ephemeral section. A permanent stage height recorder and rain gauge 6 km upstream of the study reach provided continuous flow and rainfall data (http://ecan.govt.nz/services/online-services/monitoring/river-flows/Pages) (Figure 1b). The river has a wandering planform in the study reach, with frequent avulsions, multiple channels, and many bars and islands (Larned *et al.* 2008).

Scour pools are common features in the perennial and ephemeral sections of the upper Selwyn River. The study reach generally has 15-20 distinct scour pools; the precise number varies between years due to interannual variation in flow and sediment transport regimes (authors' unpublished data). While there is a wide range of hydroperiods across pools in the ephemeral section of the Selwyn River, we have observed no perennial pools in this section, probably due to rapid downward seepage and rapid evaporation. Repeated observations of the scour pool system revealed a regular progression of stages during reach drying: declining surface flow into and out of each pool, "stranding" (cessation of surface inflow and outflow), declining water depth and surface area, and complete drying. Due to variable subsurface inflow, some pools refill and dry several times during individual stranded periods. Our preliminary observations suggested that the frequency of complete drying and the durations of emersed periods in pools in the ephemeral section varied with distance from the perennial section. The water depth fluctuations noted above indicate that there are vertical gradients in the frequency and duration of substrate emersion within pools. In the perennial section, we observed surface flow into and out of scour pools throughout the study, and there were no changes in wetted pool depths below the pool rims.

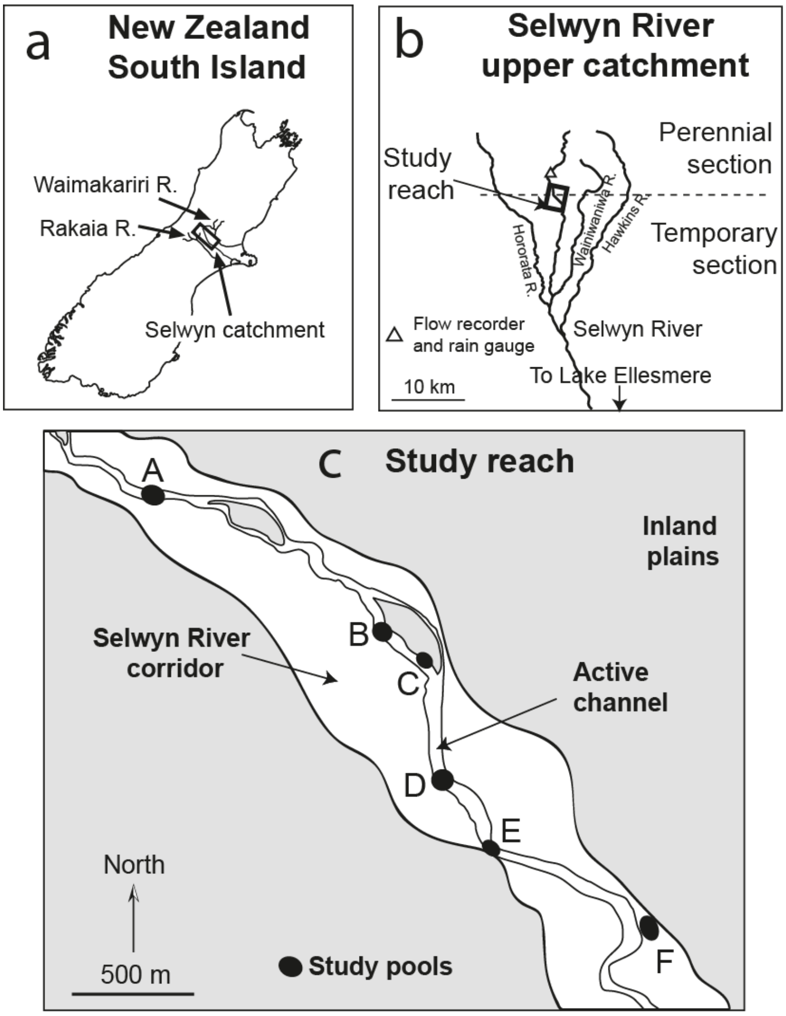

Figure 1 Map of the Selwyn River catchment (a), the study reach (b), and the scour pools (c) labelled A-F.

Pool hydrology

Six scour pools were selected for the leaf-litter study, five in the ephemeral section and one in the perennial section (Figure 1c). The pools were 0.5 to 2.6 km apart. The mean ± 1 SD pool dimensions were 22.1 ± 13.1 m length (parallel to long axis of channel), 9.9 ± 8.9 m width, and 1.2 ± 0.2 m depth. A capacitance water level recorder (Odyssey Dataflow Systems, Christchurch, New Zealand, model ODYWL15) inside a screened PVP pipe was attached to a steel post driven into the deepest point of each pool (Figure 2). An iButton temperature recorder (Embedded Data Systems, Lawrenceburg, KY, USA) was attached to the base of each water level recorder. The recorders were deployed from 27 January to 1 March 2010 and logged water level and temperature data at 15 and 10 min intervals, respectively. Abrupt changes in the amplitude of diurnal temperature fluctuations indicated the times at which a pool dried completely or was rewetted. Elevation profiles of each pool, and the elevations of the water surface and the water level recorder in each pool were measured on 11 February 2010 with a Trimble 5700 real-time kinematic global positioning system (RTK-GPS) with ± 2-cm vertical accuracy (Trimble Navigation Ltd., Sunnyvale, CA, USA). Elevation profiles were based on six approximately equally-spaced depth contours, distributed from the highest point on the rim of each scour pool to the deepest point in the pool (Figure 2). A 1-m long steel cable was laid along each depth contour; the ends of the cables were accurately positioned with RTK-GPS and they were anchored with stainless steel rods. The cables were used to secure leaf-litterbags along each contour. The elevations of depth contours were combined with the water level recorder data to determine immersion and emersion times for the litterbags.

Field procedures

We used recently-fallen leaves of riparian cottonwood (*Populus* sp.) trees for the leaf litter breakdown experiment. Cottonwood is a widespread, introduced riparian tree in New Zealand, and is the most common riparian tree along the upper Selwyn River (Larned *et al.* 2008). Leaves were collected from gravel bars along the upper Selwyn River on one day in March 2009 (austral autumn), mixed, and stored in light-proof bags. For litterbag preparation, petioles were removed and the leaves were oven-dried at 105 °C for 72 h, weighed into 3.2 ± 0.2 g (mean ± SD) portions, rehydrated for 30 min, and enclosed in plastic-mesh bags (15 x

15 cm; 16-mm^2 holes). The litterbags were closed loosely with monofilament nylon line and labeed with numbered plastic tags.

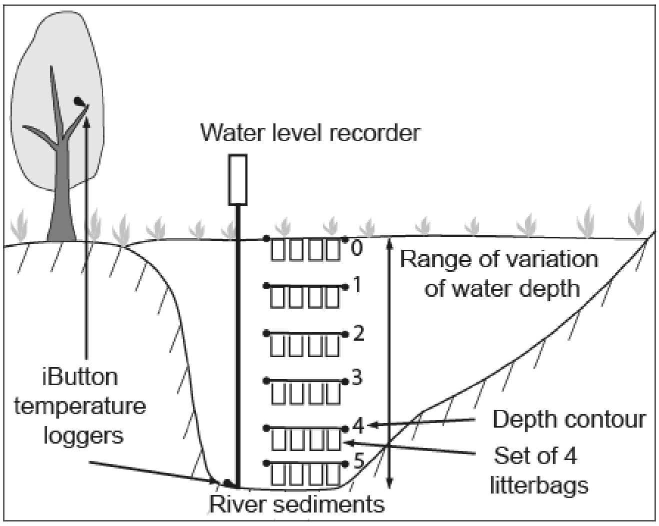

Figure 2 Schematic cross-section of a scour pool showing the positions of depth contours, litterbags, and water level and temperature recorders.

On 1 February 2010, 162 litterbags were installed in the scour pools. In each of the six pools, four litterbags were attached to the cable on each of the six depth contours (Figure 2). Three additional litterbags were placed in each pool and removed one minute later (Date 1); these bags were used to estimate handling losses and to indicate starting conditions. The remaining litterbags were retrieved 3 (Date 2), 10 (Date 3), 18 (Date 4) and 29 (Date 5) days after the start of the experiment. On each removal date, a randomly selected bag was collected from each depth contour in each pool. Water temperature, pH, dissolved oxygen (DO) and electrical conductivity were measured in each wetted pool on each collection date using hand-held WTW meters (WTW, Weilheim, Germany). Water velocity was measured at each submerged depth contour portions of each pool on each collection date, with a Flo-Mate 2000 velocity meter (Hack/Marsh-McBirney, Fredrick, MD, USA) and wading rod.

Laboratory procedures

Upon retrieval, triplicate 5-mm diameter disks were cut from leaves in each litter-bag with a cork borer for microbial activity measurement (see below). The remaining material was rinsed with tap water in a 250-µm mesh sieve to remove sediment, biofilm and invertebrates. The

leaf material was then dried (at 105°C for 72 h) and weighed. Invertebrates retained on the sieve were preserved in 70% ethanol for identification and enumeration (see below).
Hydrolysis of fluorescein diacetate (FDA) by non-specific esterases was used as an indicator of microbial activity. FDA hydrolysis on leaf disks was measured using the procedure of Fontvieille *et al.* (1992) with some modifications. Briefly, the 3 leaf disks from each litterbag were transferred to sterile glass vials (ashed at 550°C for 90 min) with 3 ml of phosphate buffer (pH 7.6) and 0.1 ml FDA solution immediately after they were cut from the leaves. Vials were incubated for 60-100 min at room temperature in darkness until a faint green color appeared. The reaction was stopped by adding 3 ml acetone. The supernatant was centrifuged at 4000 RPM for 10 min and transferred to a quartz cuvet. Absorbance was measured at 490 nm with a Uvikon 860 spectrometer (Kontron Instruments, Hayward, CT, USA) and converted to μmole fluorescein using a standard curve. The leaf disks were then dried at 105°C for 72 h and weighed. Microbial activity was expressed as μmole FDA hydrolyzed per hour per gram leaf dry mass.

Aquatic and terrestrial macroinvertebrates in the litterbags were identified to the lowest possible taxonomic level; genus or species for most insects, and family or order for other taxa. All of the invertebrates were counted and classified as aquatic or terrestrial. Aquatic invertebrates were further classified into functional feeding groups, based on Chadderton (1988) and an online database of New Zealand freshwater invertebrate traits (http://fbis.niwa.co.nz). Feeding group information for terrestrial taxa is very limited at our identification levels (generally order), so taxa containing known leaf-shredding species were classified as potential shredders. Invertebrate densities were expressed as individuals per gram remaining leaf litter dry mass (individual g^{-1} LL).

Data analyses

Immersion-emersion dynamics

The depth contours and corresponding litterbags in each pool were classified into one of three hydrological classes on the basis of water level fluctuations during the 29-d experiment: "immersed" contours were submerged throughout the study; "intermittent" contours dried or rewetted at least once; "emersed" contours were dry throughout the study. In addition, two quantitative hydrological metrics were computed for the depth contours in the intermittent class: number of emersed periods (NEP) during the study period, and cumulative emersed duration (CED, the total number of days of emersion during the study period).

Leaf litter breakdown

Leaf-litter breakdown was quantified using the dry leaf mass remaining on each collection date, corrected for the estimated mass lost at the start of the experiment (date 1) and for the mass of leaf disks removed for microbial activity measurements. We assumed that the mass biofilm and sediment remaining on leaves was negligible. Comparisons of percent litter mass remaining at the end of the study in the three hydrological classes were made with a Kruskal-Wallis test and non-parametric pair-wise multiple comparisons. To determine whether the proportions of litter mass lost in each hydrological class were statistically significant, percent remaining mass at date 2 and at the end of the study were compared with Kruskal-Wallis tests. Breakdown rate coefficients (k) per day were calculated for the litterbags at each depth contour assuming an exponential decay model $W_t/W_o = e^{-kt}$, where Wo is the initial leaf litter mass, and Wt is the mass remaining at time t (Bärlocher 2007). Relationships between k and NEP and CED in the intermittent class were assessed with linear and non-linear regressions. To test for a pool effect influencing breakdown in intermittent litterbags, differences in k among pools containing intermittent depth contours were tested using a Kruskal-Wallis test.

Physico-chemistry, microbial activity and invertebrate assemblages

Among pool differences in water temperature, pH, DO, electrical conductivity, flow velocity were analysed by Kruskal-Wallis tests, using dates as replicates. Microbial activity, invertebrate taxonomic richness, and total density and density of leaf-shredding invertebrates at the end of the experiment were compared across the three hydrological classes using Kruskal-Wallis tests and non-parametric pair-wise multiple comparisons. To test whether microbial activity and invertebrate assemblages in each hydrological class varied during the study, microbial activity, terrestrial invertebrate taxonomic richness, total invertebrate density and total shredder density at date 2 and at the end of the experiment were compared with Kruskal-Wallis tests. Relationships between microbial activity, invertebrate taxonomic richness, total density and density of aquatic and terrestrial leaf-shredding invertebrates in intermittent litterbags, and NEP and CED were examined using linear and non-linear regressions. To examine the potential effect of wetted habitat contraction on invertebrate densities, mean invertebrate densities for each immersed depth contour were regressed against the difference between maximum and minimum water levels in the corresponding pools.

Relations among microbial activity, invertebrate assemblages and leaf litter breakdown

Multiple linear regression models were used to assess the relative importance of microbial activity and leaf-shredding invertebrates on leaf litter breakdown in each hydrological class. Log-transformed k values were used to improve regression residual normality.

All statistical analyses were carried out using R software (http://cran.r-project.org/). The significance level (p) for statistical analyses was 0.05.

RESULTS

Immersion-emersion dynamics

River flow at the recorder upstream of the study reach steadily declined from 1.2 $m^3 s^{-1}$ at the start of the experiment to 0.6 $m^3 s^{-1}$ on day 19, increased to 3.1 $m^3 s^{-1}$ on day 20, then declined until the end of the study. The flow pulse on day 20 followed a convective storm on day 18, during which 16 mm of rain fell at the recorder site. There was a total of 44 mm of rain during the study, distributed over 10 days with measureable rainfall. Flow variation during the study caused water level fluctuations in the scour pools. Two pools (A and B) contained water throughout the study period, but the uppermost depth contours were dry throughout the study, and the litterbags from those contours were classified as emersed (Table 1). In one pool, (F) all contours were dry throughout the study, and litterbags from those contours were classified as emersed. Three other pools (C, D and E) dried and filled completely several times, and litterbags from each contour was classified as intermittent, except the uppermost depth contours which were dry throughout the study, and the litterbags from those contours were classified as emersed. A compilation of the water level recorder data for all six pools indicated that 10 depth contours were continuously immersed, 14 were continually emersed, and 12 were intermittent (Table 1). The number of emersed periods (NEP) at intermittent contours ranged from 1 to 8 (mean ± SD: 3.1 ± 2.6) and the cumulative emersed durations (CED) at these contours ranged from 0.2 to 27.4 days (mean ± SD: 15.3 ± 12.9) (Table 1).

Leaf litter breakdown

Across all contours, the percentage of leaf litter mass remaining in litterbags at the end of the experiment ranged from 29.6 to 92.9 % (mean ± SD: 76.8 ± 18.3) (Figure 3), and breakdown rate coefficients (*k*) ranged from 0.0032 to 0.0443 (mean ± SD: 0.0168 ± 0.0135). The percent of leaf litter mass remaining at the end of the experiment differed significantly between the three hydrological classes (Kruskal-Wallis test, $p < 0.001$): the immersed litterbags had the least mass remaining and the emersed litterbags had the most (multiple comparison tests, $p < 0.05$ for all tests, except the emersed-intermittent comparison) (Figure 3). There was a statistically significant decrease in percent litter mass remaining in each hydrological class over the course of the study (Kruskal-Wallis tests, $p < 0.05$). Within the intermittent litterbags, breakdown rate coefficients (*k*) ranged from 0.0035 to 0.0369 (mean $\pm$ SD: 0.0142 $\pm$ 0.0103). *k* decreased exponentially with increasing CED across all pools (Figure 4). There was no detectable relationship between *k* and NEP (Figure 4). There were no detectable differences in *k* between the three pools containing intermittent contours.

Table 1. Hydrological class, number of emersed periods (NEP) and cumulative emersed duration (CED) for each depth contour in each of six scour pools. Contours are numbered from shallowest (0) to deepest (5), as indicated in Figure 2.

Pools	Contours	Hydrological classes	NEP	CED (days)
A	0	emersed	1.0	29.0
	1	immersed	0.0	0.0
	2	immersed	0.0	0.0
	3	immersed	0.0	0.0
	4	immersed	0.0	0.0
	5	immersed	0.0	0.0
B	0	emersed	1.0	29.0
	1	immersed	0.0	0.0
	2	immersed	0.0	0.0
	3	immersed	0.0	0.0
	4	immersed	0.0	0.0
	5	immersed	0.0	0.0
C	0	emersed	1.0	29.0
	1	emersed	1.0	29.0
	2	intermittent	8.0	24.3
	3	intermittent	2.0	1.7
	4	intermittent	1.0	0.7
	5	intermittent	1.0	0.5
D	0	emersed	1.0	29.0
	1	emersed	1.0	29.0
	2	intermittent	5.0	18.9
	3	intermittent	7.0	10.6
	4	intermittent	6.0	7.6
	5	intermittent	1.0	0.2
E	0	emersed	1.0	29.0
	1	emersed	1.0	29.0
	2	intermittent	1.0	27.4
	3	intermittent	1.0	26.9
	4	intermittent	2.0	22.8
	5	intermittent	2.0	22.6
F	0	emersed	1.0	29.0
	1	emersed	1.0	29.0
	2	emersed	1.0	29.0
	3	emersed	1.0	29.0
	4	emersed	1.0	29.0
	5	emersed	1.0	29.0

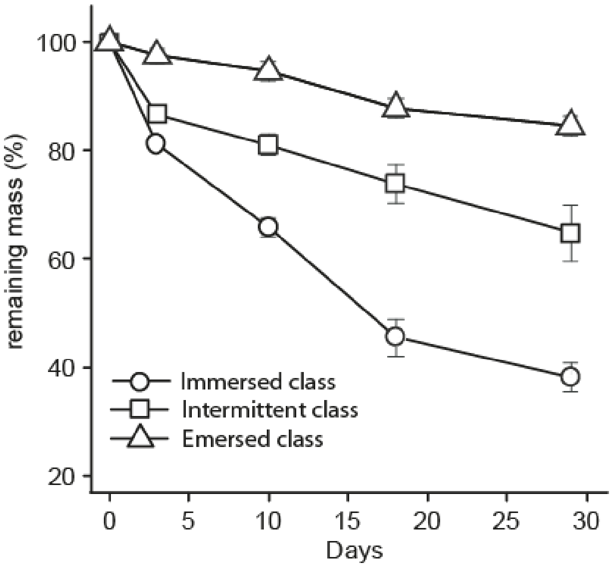

Figure 3 Temporal changes in percent leaf litter mass remaining in litterbags from three hydrological classes. Error bars are one standard deviation.

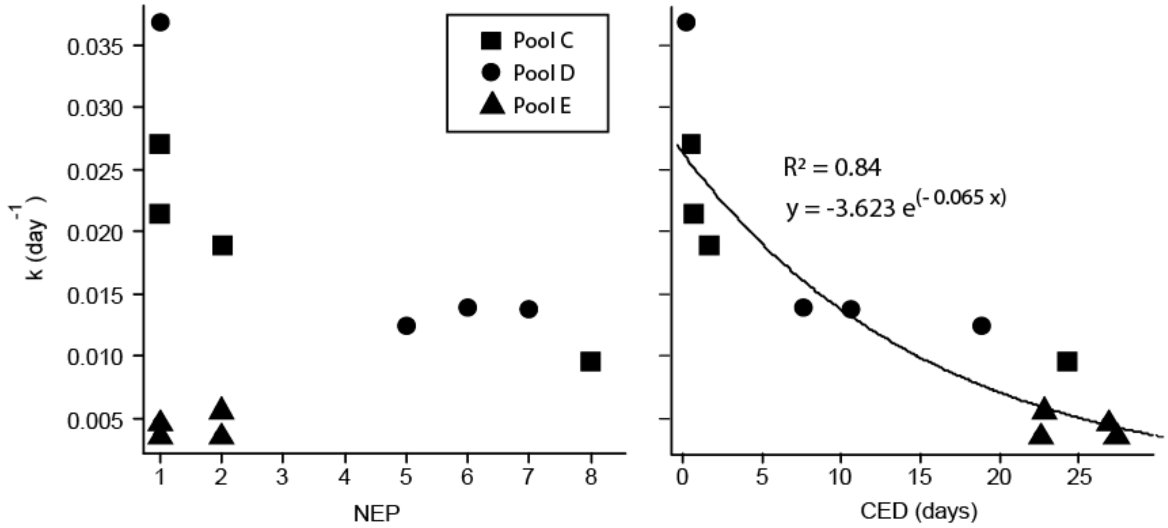

Figure 4 Relationships between leaf litter breakdown rate coefficients (k) and number of emersed periods (NEP) and cumulative emersed duration (CED) in intermittent litterbags. The line represents the fit to the statistically significant non-linear regression.

Physico-chemistry and microbial activity

Water temperature during the study ranged from 13.9 to 20.5 °C (mean ± SD: 16.5 ± 1.8), pH from 5.8 to 7.8 (6.5 ± 0.6), DO from 6.6 to 10.1 mg L^{-1} (8.1 ± 1.1), electrical conductivity from 90.0 to 108.8 μS cm^{-1} (101.1 ± 10.9) and flow velocity from 0.00 to 0.75 m s^{-1} (0.10 ± 1.16) (Table 2). Air temperature at the study reach ranged from 7.6 to 32.5 °C (17.6 ± 4.5). There were no detectable differences among pools in physico-chemistry or water velocity (Kruskal-Wallis tests, $p > 0.05$).

Microbial activity on leaf litter (as FDA hydrolysis) ranged from 0.22 to 5.50 μmol g^{-1} h^{-1} (mean ± SD: 1.39 ± 1.08) (Figure 5). At the end of the study, microbial activity was higher in immersed litterbags than in the intermittent and emersed litterbags (multiple comparison tests, $p < 0.05$ for all tests) (Figure 5). Microbial activity in the immersed and intermittent litterbags increased over the course of the study (Kruskal-Wallis tests, $p < 0.05$), but did not increase in the emersed litterbags (Kruskal-Wallis test, $p > 0.05$). Microbial activity in intermittent litterbags decreased linearly with increasing CED (Figure 6). There was no detectable linear or curvilinear relationship between microbial activity and NEP (Figure 6).

Table 2. Water temperature (T_{wat}), pH, dissolved oxygen (DO), electrical conductivity (EC), and flow velocity for each of six scour pools on each litterbag removal date. T_{wat}, pH, DO and EC values are from single measurements. Flow velocities are means of measurements at each wetted depth contour.

Pool	Date	T_{wat}	pH	DO	EC	Velocity
A	1	18.3	7.2	7.9	101	0.24
	2	19.8	7.0	8.8	100	0.03
	3	15.1	6.2	9.4	98.1	0.03
	4	15.1	5.8	9.1	102	0.02
	5	13.9	6.5	8.9	102	0.03
B	1	17.2	7.5	7.6	100	0.22
	2	17	7.0	7.0	98.6	0.03
	3	15.3	6.3	10.1	103	0.04
	4	15	5.8	9.1	101	0.04
	5	15	6.4	8.7	103	0.00
C	1	17.8	6.7	9.3	103	0.00
	2	20.5	6.7	7.1	95	0.00
	3	17	6.0	7.8	105	0.00
	4	16.7	6.2	7.0	104	0.00
	5	16.7	7.4	7.0	104	0.00
D	1	16.2	7.5	11.1	101	0.28
	2	18.5	7.8	7.8	90.2	0.04
	3	16.5	6.0	6.6	104	0.00
	4	15.4	6.3	6.0	99.6	0.02
	5	17	7.1	5.6	109	0.00
E	1	16	7.4	10.5	100	0.33
	2	Dry	Dry	Dry	Dry	Dry
	3	Dry	Dry	Dry	Dry	Dry
	4	Dry	Dry	Dry	Dry	Dry
	5	Dry	Dry	Dry	Dry	Dry
F	1	Dry	Dry	Dry	Dry	Dry
	2	Dry	Dry	Dry	Dry	Dry
	3	Dry	Dry	Dry	Dry	Dry
	4	Dry	Dry	Dry	Dry	Dry
	5	Dry	Dry	Dry	Dry	Dry

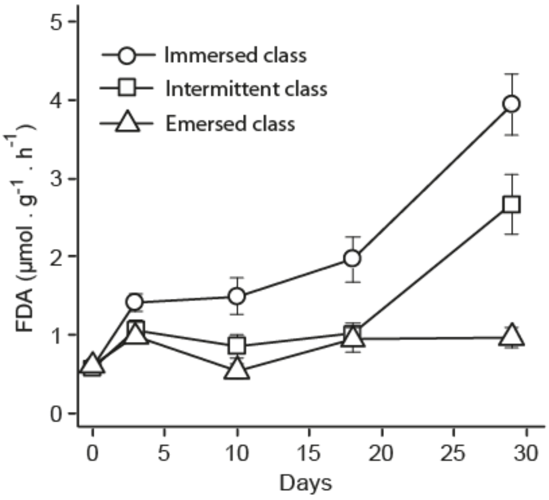

Figure 5 Temporal changes in leaf-litter microbial activity in litterbags from three hydrological classes.

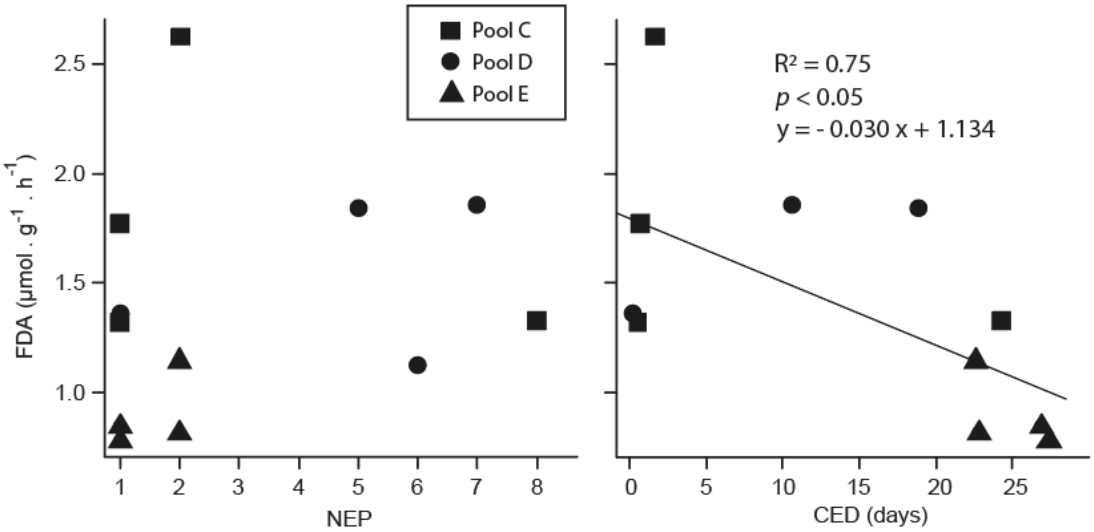

Figure 6 Relationships between microbial activity and number of emersed periods (NEP) and cumulative emersed duration (CED) in intermittent litterbags. The line represents the fit to the statistically significant linear regression.

Invertebrate assemblages

In total, 5959 invertebrates were collected from litterbags. These individuals represented 31 aquatic taxa and 15 terrestrial taxa (Table 3). Terrestrial taxa had low densities (mean ± SD: 1.2 ± 2.1 individual g^{-1} LL) and represented < 4 % of the total density. *Olinga feredayi* and *Physa acuta* were the only aquatic shredders but they comprised 20.2 % of the invertebrates collected. Three terrestrial taxa (Acarina, Collembola, and Coleoptera) were potential shredders; they comprised < 2 % of the total and < 30 % of the terrestrial invertebrates collected (Table 3).

Taxonomic richness, total invertebrate density and shredder density (both terrestrial and aquatic) differed among hydrological classes at the end of the experiment (Kruskal-Wallis, $p < 0.05$). Each of the three invertebrate variables was higher in immersed litterbags than in intermittent and emersed litterbags (multiple comparison tests, $p < 0.05$ for all tests) (Figure 7). Taxonomic richness, total invertebrate density, and total shredder density increased over the course of the study in the immersed and intermittent litterbags (Kruskal-Wallis tests, $p < 0.05$) but did not change significantly in the emersed litterbags (Kruskal-Wallis test, $p > 0.05$) (Figure 7).

Total invertebrate density and taxonomic richness decreased linearly with increasing CED in intermittent litterbags ($R^2 = 0.6$ and 0.7, respectively, $p < 0.05$). Aquatic shredder density decreased exponentially with CED (Figure 8). However, no relationships were detected between terrestrial shredder density and CED or NEP (Figure 8). No relationships were detected between total invertebrate density, taxonomic richness or aquatic shredder density, and the maximum difference in water levels in the corresponding pools ($R^2 < 0.2$, $p > 0.05$).

Relations among microbial activity, invertebrate assemblages and leaf litter breakdown

There was a positive effect of aquatic shredder density on k in immersed litterbags, but no detectable effect of microbial activity on k (multiple linear regression, Table 4). There were significant, positive effects of both microbial activity and total shredder density on k in the intermittent litterbags (Table 4). There was a significant, positive effect of microbial activity on k in the emersed litterbags, but no detectable effect of terrestrial shredder density (Table 4). There were no significant interactions between shredder density and microbial activity within each class (Table 4).

Table 3. Mean, minimum and maximum invertebrate density (individuals.g^{-1} leaf litter dry mass), and frequency of occurrence (FO) of taxa. A: aquatic; T: terrestrial. *: aquatic leaf-shredding invertebrate; **: terrestrial leaf-shredding invertebrate.

Taxa		Habitat	Mean	Min	-	Max	FO (%)
Annelida	Unidentified	T	0.0	0	-	0.9	3.1
	Oligochaeta	A	2.7	0	-	77.8	23.1
Mollusca	*Physa acuta*	A	0.2	0	-	6.0	7.7
	Potamopyrgus antipodarum	A	2.9	0	-	54.4	38.5
Crustacea	Cladocera	A	0.6	0	-	21.2	18.5
	Copepoda	A	0.1	0	-	1.3	7.7
	Cyclopoida	A	0.4	0	-	6.1	20.8
	Ostracoda	A	1.7	0	-	22.7	41.5
Arachnida	Acarina **	T	0.3	0	-	7.0	16.2
	Araneae	T	0.0	0	-	0.5	4.6
Collembolla **		T	0.6	0	-	19.9	19.2
Coleoptera	Caribidae (adult)	T	0.1	0	-	1.9	7.7
	Curculionoidae	T	0.0	0	-	0.7	2.3
	Elmidae	A	0.0	0	-	1.5	2.3
	Staphylinidae (adult)	T	0.1	0	-	5.8	8.5
	Unidentified (adult)	T	0.0	0	-	0.6	6.9
	Unidentified (larva) **	T	0.0	0	-	0.6	0.8
Dermoptera		A	0.0	0	-	0.4	0.8
Diptera	Chironomidae (larva)	A	9.1	0	-	129.2	53.8
	Chironomidae (adult)	T	0.0	0	-	0.8	0.8
	Chironomidae (nymph)	A	0.2	0	-	4.5	16.2
	Chironomidae (desiccated)	A	0.1	0	-	7.0	0.8
	Unidentified (adult)	T	0.0	0	-	1.6	6.9
	Unidentified (larvae)	A	0.0	0	-	1.1	3.1
Ephemeroptera	*Deleatitium* sp.	A	0.1	0	-	1.2	6.2
	Neozephlebia sp.	A	0.0	0	-	0.7	4.6
	Zephlebia sp.	A	0.0	0	-	1.4	5.4
Megaloptera	*Archichauliodes diversus*	T	0.1	0	-	2.3	5.4
Plecoptera	*Stenoperla prasina*	A	0.0	0	-	0.9	0.8
Thysanoptera		T	0.0	0	-	0.4	1.5
Trichoptera	*Aoteapsyche* sp.	A	0.0	0	-	0.4	0.8
	Oxyethira albiceps (desicated)	A	0.3	0	-	39.3	2.3
	Helicopysche sp.	A	0.0	0	-	1.0	1.5
	Hudsomema sp.	A	0.1	0	-	3.1	10.0
	Neurochorema confusum	A	0.0	0	-	1.5	1.5
	Olinga feredayi *	A	6.0	0	-	69.4	45.4
	Oxyethira albiceps	A	2.9	0	-	213.2	28.5
	Psilochorema sp.	A	0.0	0	-	1.0	4.6
	Olinga feredayi (pupa)	A	0.0	0	-	1.1	2.3
	Oxyethira albiceps (pupa)	A	1.1	0	-	129.8	4.6
	Pycnocentrodes sp. (pupa)	A	0.0	0	-	0.9	0.8
	Pycnocentria sp.	A	0.1	0	-	3.1	8.5
	Pycnocentrodes sp.	A	0.1	0	-	2.6	4.6
	Unidentified (larva)	A	0.0	0	-	1.5	3.1

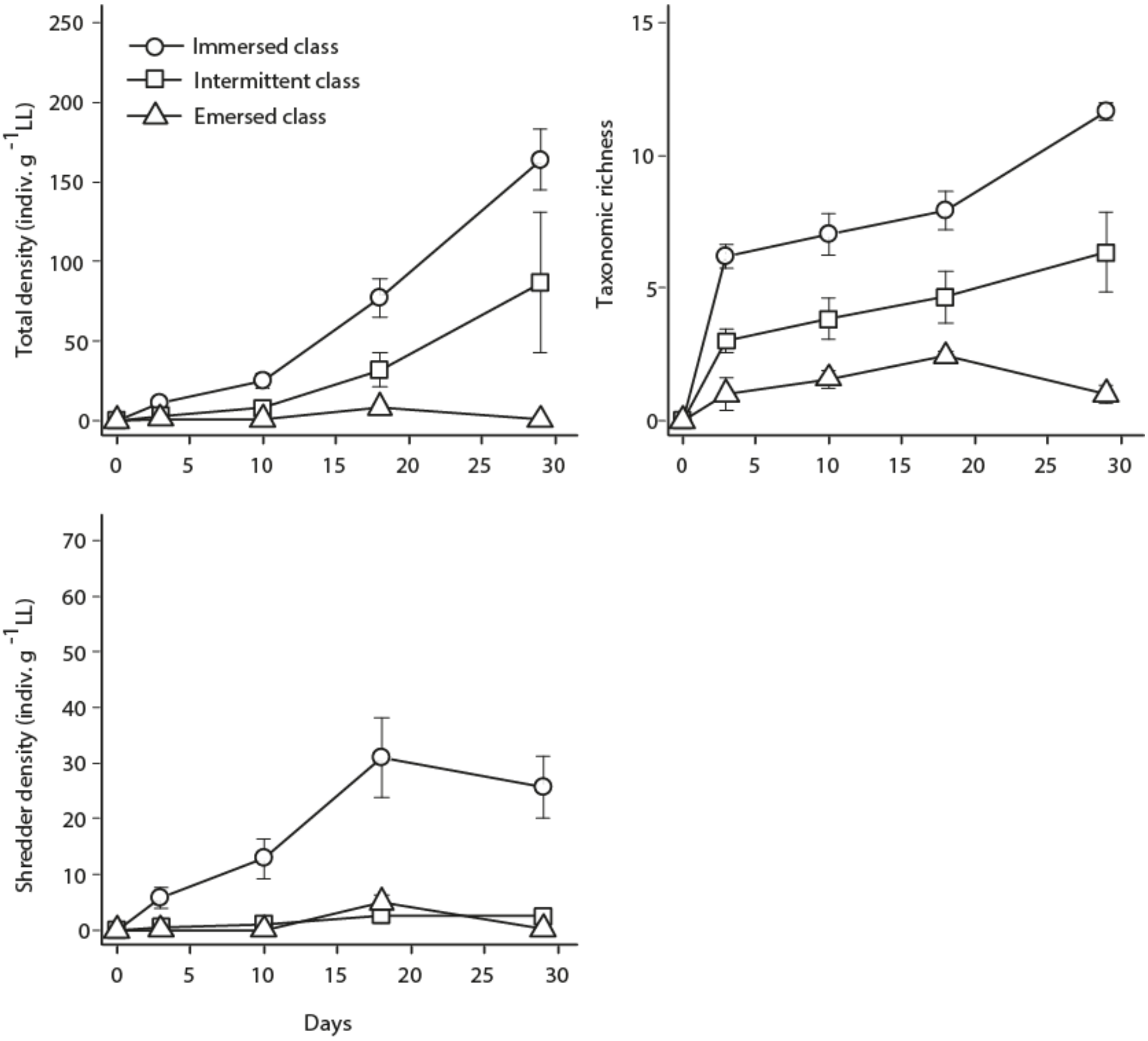

Figure 7 Temporal changes in invertebrate taxonomic richness, total invertebrate density and total shredder density in litterbags from the three hydrological classes.

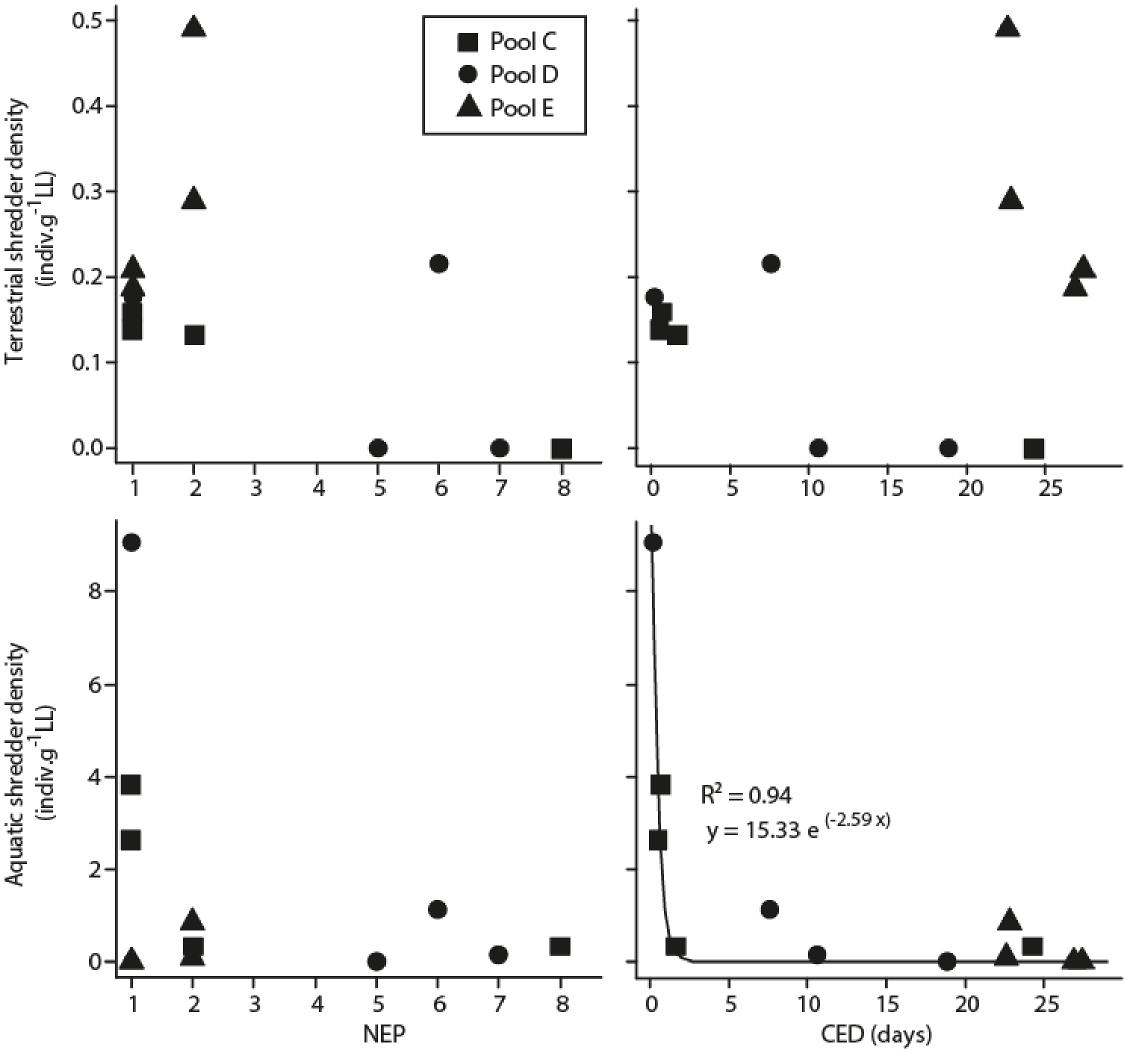

Figure 8 Relationships between terrestrial and aquatic shredder density and number of emersed periods (NEP) and cumulative emersed duration (CED) in intermittent litterbags. The line represents the fit to the statistically significant non-linear regression.

Table 4. Coefficient values, standard errors (SE) and t-values for multiple linear regressions of microbial activity and leaf-shredding invertebrate density on *k* within hydrological classes. * indicates significant relationships ($p < 0.05$)

	coefficient	SE	t
Immersed class ($R^2 = 0.73$, $p < 0.05$)			
Microbial activity	-0.0073	0.0449	-0.164
Leaf-shredding invertebrate density	0.0116	0.0031	3.755 *
Interactive effect	-0.0011	0.0072	-0.149
Intermittent class ($R^2 = 0.76$, $p < 0.05$)			
Microbial activity	0.8584	0.2402	3.574*
Leaf-shredding invertebrate density	0.1932	0.0488	3.957 *
Interactive effect	-0.6463	0.3212	-2.012
Emersed class ($R^2 = 0.86$, $p < 0.05$)			
Microbial activity	0.5976	0.2618	2.282 *
Leaf-shredding invertebrate density	0.0335	0.0656	0.511
Interactive effect	-0.3982	0.3023	-1.317

DISCUSSION

Leaf litter breakdown

The results of this study indicate that natural variation in immersion and emersion has strong effects on leaf litter breakdown. Within a single river reach, litter breakdown in permanently immersed locations was faster than in permanently emersed and intermittent locations, and breakdown in intermittent locations was inversely related to the cumulative duration of emersion. These findings, and those of Datry *et al.* (2011), are among the first to test the conceptual model proposed by Larned *et al.* (2010a), in which temporary rivers function as punctuated biogeochemical reactors. In this model, leaf litter and other forms of particulate organic matter (POM) are transferred by flow pulses to "reserves" downstream (*e.g.* scour pools and other sites where material is retained during flow recessions). The temporary presence of water in these reserves stimulates some biogeochemical and ecological processes, including leaf litter breakdown by aquatic microbes and invertebrates. Emersion in reserves causes the cessation of water-dependent processes, and the onset or intensification of water-independent processes such as photodegradation, fungal decomposition, and comminution by terrestrial invertebrates (Austin and Vivanco 2006; Collins *et al.*, 2008). POM is progressively processed during each cycle of transport, retention, emersion and immersion. In the conceptual model, POM processing rates are predicted to decrease during emersed periods, and increase upon re-immersion, which creates a "punctuated" temporal pattern in processing. The efficiency of POM processing is predicted to increase directly with the frequency of processing cycles. Our results are consistent with the prediction that POM processing is slower during emersed periods, but not with the prediction that POM processing increases with increasing frequencies of emersion and immersion. Instead POM breakdown in our study was strongly affected by the cumulative duration of emersion, and relatively unaffected by the frequency of emersion and immersion.

The focus of our study was the effect of immersion-emersion cycles on litter breakdown, independent of location within a river corridor. However, location is likely to affect litter breakdown indirectly, because immersion-emersion cycles vary down the lengths of river channels (Rupp *et al.* 2008, Larned *et al.* 2010b), and laterally across the river-floodplain-upland gradient (Benke *et al.* 2000, Ward *et al.* 2002). Results of field studies indicate that litter breakdown patterns on floodplains correspond to lateral variation in immersion and emersion (Andersen and Nelson 2006, Langhans *et al.* 2008). The longitudinal model of litter breakdown referred to above (including the roles of "reserves") also applies to floodplains, but in the lateral dimension. Evidence for this includes lateral gradients in the frequency and duration of floodplain inundation, lateral transport of litter across floodplains (Junk *et al.* 1989, Neatrour *et al.* 2004), and differences in the dominant mechanisms and species that control floodplain litter breakdown during immersed and emersed periods (Austin and Vivanco 2006, Collins *et al.* 2008, Gallo *et al.* 2009).

We used quantitative relationships between k and emersion to test several predictions. Our first prediction was that leaf litter breakdown rates decrease as the frequency and duration of emersed periods increase; this prediction was partly confirmed by our results, as k decreased exponentially with increasing CED in intermittent litterbags. However, k was not statistically related to NEP. Emersion duration, rather than frequency, was also reported to be the main driver of organic matter processing in rivers (Langhans and Tockner 2006). Frequent emersed periods of short duration may have less effect on leaf litter processing by aquatic invertebrates and micro-organisms than long emersed periods.

Water temperature, pH and other physico-chemical parameters have been shown to influence leaf litter breakdown in rivers (Tank *et al.* 2010). However, these parameters did not cause leaf-litter breakdown to vary among pools in our study, as among-pool differences in physico-chemical parameters and water velocity were minimal. The wetted pools were probably inter-connected by hyporheic flow, the velocity of which can be as high as 8 m h^{-1} in the study reach (Datry and Larned 2008). Rapid hyporheic flow between pools would lead to homogenization of physico-chemical parameters.

Quantitative relationships between emersion and leaf litter breakdown are rarely reported, but are needed to understand the influence of immersion-emersion cycles on POM processing and other ecosystem processes in hydrologically dynamic rivers (Maamri *et al.* 1997; Langhans and Tockner 2006; Larned *et al.* 2010a). These relationships may also be useful for river management. Flow diversion, dam operations, and other human uses of river flows can alter natural flow pulse patterns, and consequently alter immersion-emersion cycles (Tockner *et al.*

2000). There is also some evidence that river intermittency is increasing, as a consequence of increasing surface water and groundwater abstraction and climate change (Larned *et al.* 2010b). The quantitative relationships reported in this study between immersion-emersion cycles and leaf litter breakdown may be used to predict the ecological effects of altered flow regimes and increasing flow intermittency on organic matter processing.

Invertebrate colonization

The results of the experiment confirmed our second prediction, that rates of leaf litter colonization by aquatic shredders, and subsequent effects on litter breakdown, decrease with increasing cumulative emersed duration. Under immersed conditions, aquatic shredders colonized the litterbags at rates ranging from 5 to 18 individuals g^{-1}LL day^{-1}. These rates are similar to those reported from immersed sites in three New Zealand streams (Linklater 1995). Under intermittent conditions, invertebrate taxonomic richness, total invertebrate density and total shredder density all decreased with increasing cumulative emersed duration, probably because desiccation-sensitive taxa were eliminated. The two aquatic shredders found in the litterbags, *Olinga feredayi* and *Physa acuta*, abundant in permanently immersed litterbags but strongly rarefying in intermittent litterbags with increasing the cumulative duration of emersion were reported to be sensitive to desiccation (Datry *et al.* 2007; Arscott *et al.* 2010). Elimination of desiccation-sensitive shredders during emersed periods may contribute to the negative relationship we observed between litter breakdown and emersion.

The results of the experiment partly confirmed our third prediction, that terrestrial shredders and microbes would colonize and process leaf litter following emersion. Terrestrial invertebrates did colonize the litterbags, but had little effect on litter breakdown. While terrestrial invertebrates may be abundant on dry riverbeds (Uetz *et al.* 1979; Maamri *et al.* 1997; Wishart 2000; Paetzold *et al.* 2005; Steward *et al. this issue*), many are predators and leaf litter does not appear to be an important food source (Andersen and Nelson 2006). Of the 15 terrestrial taxa that occurred in our litterbags, only three (Acarina, Collembola, and Coleoptera larvae) were potential shredders, and they represented < 30% of the terrestrial invertebrate density. Terrestrial invertebrates could affect litter breakdown indirectly by preying on aquatic shredders in intermittent zones; this predation pattern has been reported from the Selwyn and other temporary rivers (Greenwood and McIntosh 2010). However, the similarity in terrestrial invertebrate densities in intermittent litterbags and permanently emersed litterbags in our study suggests that terrestrial predators were not strongly attracted to aquatic invertebrate prey after emersion.

Microbial activity and immersion-emersion dynamics

We found that microbial activity decreased exponentially with increasing CED. Reduced leaf pack moisture could be a direct cause of reduced microbial activity following emersion, as is the case for river sediments (Amalfitano *et al.* 2008, Iovieno and Bääth 2008). The absence of a detectable relationship between emersion frequency and microbial activity suggests that frequent immersion and emersion did not promote microbial activity, as has been observed in temporary wetlands (Battle and Golladay 2001). The different outcomes in our study and the wetland study may be related to dissolved oxygen concentrations, which were low during immersed periods in the wetland, and consistently high in the scour pools.

In both terrestrial (Swift *et al.* 1979; Takeda 1995) and aquatic habitats (Kirby *et al.* 1983; Baldy *et al.* 1995), leaf litter processing involves the combined action of microbes and leaf-shredding invertebrates. The results of the experiment verified our prediction that the relative importance of microbial activity on leaf litter breakdown would increase with increasing emersion time. Multiple regression models indicated a significant effect of microbial activity on k in intermittent and emersed litterbags, but not in immersed litterbags. In contrast, aquatic and terrestrial shredder density had a significant effect on litter breakdown in immersed and intermittent litterbags, but not in emersed litterbags. The absence of synergistic effects between microbial activity and invertebrates on litter breakdown in intermittent litterbags, as indicated by the non-significant interaction term, was unexpected, because leaf-shredding invertebrates generally depend on microbial colonization of leaves for nutrition (Arsuffi and Suberkropp 1988; Abelho 2008). FDA hydrolysis, which we used as a proxy for microbial decomposition, may be too crude to indicate microbe-shredder interactions (Datry *et al.* 2011). More precise and specific parameters, such as fungal activity (*e.g.* ergosterol content) or specific enzymatic activity rates (*e.g.* xylosidase and glucosidase) could improve our understanding of these interactions.

In addition to biotic processing by terrestrial invertebrates and microbes, there are several mechanisms that may control litter decomposition during emersed periods. Taketa (1995) reported that leaching of simple organic compounds (i.e. reducing sugars, phenolic substances) during rain events accounted for a 10% decrease in *Chamaecyparis obtusa* leaf mass, while faunal and microbial colonizers had no significant action. Photodegradation can enhance dry litter breakdown (Austin and Vivanco 2006), and while we did not measure solar radiation during our study, UV radiation intensity is high in New Zealand (McKenzie et al 1999). The low breakdown rates measured in emersed conditions compared to intermittent conditions in the Selwyn River suggest that leaching, photodegradation and other mechanisms involved in dry litter decomposition were not important at the time scale of our study.

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8

SYNTHÈSE, DISCUSSION ET PERSPECTIVES

Il est aujourd'hui largement reconnu que les zones de transition terrestre-aquatique influencent de manière considérable la biodiversité, les processus biogéochimiques et la productivité d'un écosystème. Pourtant, les effets des transitions terrestre-aquatique dues aux périodes d'assèchement dans les cours d'eau temporaires (C.E.T.) sont peu connus. L'essentiel des connaissances actuelles concerne les communautés aquatiques, alors que les communautés terrestres et les processus écologiques auxquels elles sont associées ont été très peu étudiés.

L'objectif de ce travail était de préciser les effets des cycles d'assèchement et de remise en eau des cours d'eau temporaires, sur les communautés d'invertébrés terrestres des lits asséchés et des zones ripariennes d'une part, et sur la dynamique de la matière organique particulaire (MOP) d'autre part.

La première partie de ce chapitre synthétise les principaux résultats obtenus lors des expérimentations de terrain, discute de leur contribution à l'amélioration des connaissances fondamentales en écologie et met en évidence leurs implications potentielles pour la gestion des cours d'eau. La deuxième partie présente trois perspectives de recherche s'inscrivant dans la continuité de ce travail de thèse et détaille des expérimentations pouvant être réalisées.

8.1. SYNTHÈSE ET DISCUSSION DES RÉSULTATS

8.1.1. Échantillonnage des communautés d'invertébrés terrestres des lits asséchés

La première étape de ce travail de thèse a consisté à tester et à comparer deux méthodes de collecte d'invertébrés terrestres afin de déterminer laquelle est la plus adaptée aux lits asséchés. Les résultats ont montré que pour estimer la richesse taxonomique et la composition des communautés d'invertébrés terrestres, la méthode dite des pièges Barber est plus rapide et plus précise que la méthode des quadrats. De plus, la méthode des pièges Barber est plus efficace pour comparer la composition des communautés entre plusieurs sites. Un nombre élevé d'échantillons est cependant nécessaire pour estimer précisément la richesse taxonomique. En utilisant les pièges Barber, le prélèvement de 8 à 11 échantillons/100 m² permet de collecter entre 70% et 80% du nombre total estimé de taxons, un pourcentage généralement jugé comme suffisant pour réaliser des comparaisons inter-sites (Delabie *et al.* 2000; Baselga & Novoa, 2006). Ces résultats concernant l'effort d'échantillonnage suggèrent que la distribution des invertébrés terrestres est très hétérogène et complexe à l'échelle locale et fortement marquée par la présence de taxons peu abondants, difficiles à échantillonner ou regrouper au sein de micro-habitats (Ellisson *et al.* 2007).

8.1.2. Les communautés d'invertébrés terrestres dans la mosaïque d'habitats des cours d'eau temporaires

Les résultats obtenus au cours de ce travail de thèse quant à l'influence des cycles d'assèchement et de remise en eau sur les invertébrés terrestres, sont directement liés à la théorie des méta-communautés (Wilson 1992, Leibold *et al.* 2004). Celle-ci conçoit l'organisation des communautés d'organismes à différentes échelles de temps et d'espace, en considérant un écosystème comme étant composé d'un ensemble de communautés liées par la dispersion de multiples espèces qui potentiellement interagissent (Chase & Leibold 2002). En vertu de cette théorie, il est possible de percevoir la mosaïque changeante d'habitats des cours d'eau temporaires comme un ensemble de patchs aquatiques et terrestres dont chacun abrite des populations d'invertébrés organisées au sein de communautés (Larned *et al.* 2010). L'emplacement et la nature des différents patchs varient dans le temps et dans l'espace en fonction de la durée et de la fréquence des assèchements. En retour, les communautés de chaque patch sont connectées entre elles, du fait de la capacité des espèces à se disperser d'un patch à l'autre. L'ensemble forme une méta-communauté.

Les C.E.T. et leurs zones ripariennes fonctionnent comme des systèmes source-puits

Les expérimentations réalisées dans l'Albarine et l'Asse montrent que les communautés d'invertébrés terrestres des lits asséchés sont des sous-échantillons des communautés ripariennes. Par conséquent, les lits asséchés ne possèdent pas de communautés d'invertébrés spécifiques. Les zones ripariennes sont constituées d'une part, de taxons qui leur sont spécifiques et d'autre part de taxons plutôt ubiquistes qui peuvent être présents à la fois dans les zones ripariennes et les lits asséchés. L'existence de relations source-puits entre les populations du cours d'eau et de la zone riparienne (Pulliam 1988) est certainement un des mécanismes principaux impliqués dans la colonisation des lits asséchés. Cela implique que l'organisation des communautés est principalement déterminée par la dispersion des espèces entre les patchs au travers d'un effet de masse et d'un mécanisme de densité-dependance (Shmida & Wilson 1985, Mouquet & Loreau 2002). Ainsi, les populations d'invertébrés terrestres se développent dans les zones ripariennes lors des périodes en eau. Suite à l'assèchement, une partie des individus émigre vers les patchs terrestres des lits asséchés, en raison d'un effet de masse et d'un mécanisme de densité-dépendance, c'est-à-dire d'une différence de densité en invertébrés entre les patchs (Shmida & Wilson 1985). Ces migrations confèrent aux zones ripariennes un rôle essentiel dans le maintien des communautés d'invertébrés des lits asséchés.

L'existence de relations source-puits dans les C.E.T. implique de concevoir les zones ripariennes comme des habitats de qualité plus élevée que les lits asséchés, notamment parce qu'ils permettent aux différentes populations de réaliser l'ensemble de leur cycle vital (Holt 1996, Pulliam 1988). En général, les organismes sont capables d'apprécier la qualité des habitats et de préférer ceux de qualité élevée, qui constitue ainsi des sources (Pulliam 1988). Cependant, la théorie des 'pièges écologiques' décrit les raisons pour lesquelles des organismes peuvent préférer des patchs 'puits' plutôt que 'sources' (Weldon & Haddad 2005, Robertson &

Hutto 2006). Les pièges écologiques sont supposés exister lorsque l'attractivité d'un habitat augmente de manière disproportionnée par rapport à sa valeur pour la survie et la reproduction des populations (Robertson & Hutto 2006). Dans l'Albarine et l'Asse, de nombreuses espèces étaient autant, voire légèrement plus abondantes dans les lits asséchés que dans les zones ripariennes (*e.g.* *Oedothorax apicatus* (Aranea), *Chaetocnema sp.* (Coleoptera), *Zorochros dermestoides* (Coleoptera)). Les lits asséchés peuvent être des habitats favorables pour les invertébrés prédateurs, en raison de leur végétation éparse qui favorise le déplacement des individus et procure un champ de vision étendu. Ils peuvent aussi favoriser la présence de certaines espèces en raison d'interactions interspécifiques plus faibles (*e.g.* compétition, prédation). En conséquence, la présence des lits asséchés pourraient favoriser le développement de certaines populations aux dépens des autres. En définitive, la perception des lits asséchés comme des pièges écologiques dépend de la capacité des invertébrés terrestres à réaliser l'ensemble de leur cycle vital dans les lits des C.E.T. et donc de résister aux remises en eau.

Dans le modèle source-puits, les patchs de nature temporaire sont caractérisés comme des puits ou des pseudo-puits, en fonction de la capacité des espèces à maintenir des populations en l'absence de dispersion depuis les sources (Watkinson & Sutherland 1995, Leibold *et al.* 2004). Les fréquences et les durées d'assèchement contrôlent la possibilité pour une population donnée de croitre dans les lits des C.E.T. Des durées d'assèchement plus longues que le cycle vital des invertébrés peuvent permettre à ces derniers de se reproduire dans les lits asséchés et de devenir à leur tour des sources pour d'autres patchs terrestres. Mais, dans tous les cas, les remises en eau provoquent une complète réorganisation de la mosaïque d'habitats et la destruction de l'ensemble des patchs terrestres du lit du cours d'eau. Ainsi, la capacité des espèces à rester en permanence dans le lit des C.E.T., en résistant aux inondations, défini le niveau de dépendance des lits asséchés vis-à-vis des zones ripariennes. L'existence de mécanismes de résistance à l'inondation, au travers de stades de dormance ou de diapause, a été rapportée pour de nombreuses espèces d'invertébrés terrestres des marais temporaires (Adis & Junk 2002, Plum 2005) et d'invertébrés aquatiques des cours d'eau (Williams & Hynes 1976, Boulton 1989, Datry *et al.* 2012). Elle demeure complètement inconnue pour les espèces d'invertébrés terrestres des lits asséchés.

Dans l'Albarine, les résultats obtenus suggèrent que les flux d'invertébrés terrestres entre le lit du C.E.T. et les zones ripariennes s'inversent lors des remises en eau et que les lits asséchés deviennent temporairement des sources. Deux stratégies permettent aux invertébrés terrestres d'émigrer vers les zones ripariennes pour résister aux inondations. Premièrement, certaines espèces perçoivent les précipitations comme un signal indiquant l'arrivée d'une crue et déplacent vers les habitats plus élevés (Lytle & White 2004, Lambeets *et al.* 2008). Deuxièmement, les invertébrés terrestres peuvent résister à l'inondation, *via* différentes stratégies, par exemple en flottant avec les débris organiques, en trouvant refuge sous les pierres ou en respirant à l'aide de bulles d'airs (Boumezzough & Musso 1983, Lambeets *et al.* 2008). Dans l'Albarine, les densités en invertébrés terrestres transportés dans le front de remise en eau dépassaient les 3000 individus/m^3 et étaient près de 200 fois supérieures aux quantités transportées en moyenne par les cours d'eau pérennes, même en période de crue (Rincon & Lobon-Cervia 1997, Tockner & Waringer 1997, Romaniszyn *et al.* 2007). Ce résultat montre que, de toute évidence, les taux de mortalité dans les lits asséchés sont très élevés. Toutefois, de nombreux taxons ont été collectés encore vivants, et sont donc susceptibles de regagner les zones ripariennes. Ainsi, le rôle des remises en eau dans l'organisation des communautés d'invertébrés est certainement double. D'une part, elles agissent comme un filtre sélectionnant les espèces capables de résister à la remise en eau. D'autre part, elles dispersent les espèces entre les différents habitats des zones ripariennes. En conséquence, les remises en eau peuvent favoriser le développement de certaines populations d'invertébrés aux dépens d'autres et ainsi modifier les interactions entre les espèces au sein des communautés des zones ripariennes. De plus, l'inversion des flux de migration pendant la remise en eau pourrait générer un apport important d'invertébrés dans les zones ripariennes. Cet apport pourrait faire croitre le nombre d'individus au-delà de celui que les zones ripariennes peuvent normalement supporter et fournir une réserve d'individus disponible pour la colonisation des lits asséchés lors des assèchements suivant. En conséquence, les zones ripariennes et les lits asséchés sont certainement des habitats complémentaires et interdépendants.

Des communautés homogènes le long des lits asséchés

Dans sa dimension longitudinale, un cours d'eau temporaire se structure en une succession hétérogène de patchs aquatiques et terrestres qui évolue dans l'espace et dans le temps, en fonction de la durée et de la fréquence des assèchements (Datry *et al.* 2012, **Annexe 2**) Chacun de ces patchs présente un ensemble de conditions environnementales qui lui est propre (Stanley *et al.* 1997, Larned *et al.* 2010). Celles-ci influencent la composition des communautés qu'ils abritent. Suivant la capacité des espèces à habiter un ou plusieurs patchs différents, il résulte une plus ou moins grande diversité de communautés. L'étude de la composition des communautés d'invertébrés terrestres entre différents sites (ou patchs) de l'Albarine, répartis le long d'un gradient de durée d'assèchement, montre des variations relativement faibles : près de 70 % de la richesse totale des taxons communs (> 0.3% des abondances) était due à des variations de composition au sein des sites. En conséquence, la durée d'assèchement n'est certainement pas un facteur clef de la distribution des organismes dans les C.E.T.

La variation de la composition des communautés d'invertébrés terrestres le long des C.E.T. contraste avec celle des communautés d'invertébrés aquatiques. Les patchs aquatiques sont fortement dépendants les uns des autres (Datry *et al.* 2007, Arscott *et al.* 2010, Datry *et al. in review).* Les gradients longitudinaux d'assèchement éliminent progressivement les espèces aquatiques les moins résistants à la dessiccation, alors que les refuges pérennes (*e.g.* secteurs pérennes, mouilles déconnectées) alimentent les patchs aquatiques successifs lors des remises en eau. La dispersion entre les patchs se fait essentiellement par dérive au sein de la masse d'eau et par voie aérienne pour certaines espèces. Comme les patchs qui s'assèchent le plus longtemps sont aussi les plus éloignés des refuges, les patchs aquatiques constituent une succession de 'puits' pouvant devenir des sources pour les patchs environnants. En conséquence, les patchs les plus éloignés des refuges sont des sous-échantillons des patchs les plus proches. L'organisation des communautés d'invertébrés terrestres dans les lits asséchés est, en revanche, dépendante des zones ripariennes. C'est donc la dimension latérale qui joue un rôle primordial dans la composition des communautés. Les patchs 'sources' des zones ripariennes sont certainement très connectés les uns aux autres, *via* la dispersion des espèces par voie aérienne et par les remises en eau ou les crues. Il en découle une grande homogénéité de la composition des communautés le long des lits asséchés. En revanche, en raison de différences entre les habitats des lits asséchés et des zones ripariennes, la composition des assemblages ne converge pas avec la durée d'assèchement (**Annexe 2**). Ces résultats impliquent que les processus et les mécanismes qui contrôlent la structure et la composition des communautés d'invertébrés terrestres et aquatiques dans les lits asséchés interviennent à des échelles de temps et d'espaces différentes. Ainsi, les modèles conceptuels développés sur les communautés aquatiques dans les C.E.T. (Larned *et al.* 2010) ne sont pas transposables aux communautés terrestres.

8.1.3. Effets en cascade des assèchements sur les communautés ripariennes

L'eau et les insectes aquatiques émergents d'un cours d'eau sont des ressources pour les populations d'invertébrés terrestres prédateurs et hygrophiles (i.e. avec des préférences pour les habitats humides) des zones ripariennes, qui en retour modifient la composition des communautés d'organismes et la dynamique des chaines alimentaires (Baxter *et al.2005*).

L'expérience menée dans la rivière Albarine a montré que les communautés d'invertébrés ripariens possèdent de fortes capacités de résistance et de résilience, vis-à-vis de l'assèchement. Les mécanismes de résistance sont liés aux traits d'histoire de vie des espèces. Le fait que la diminution de la diversité et de l'abondance des invertébrés ripariens soit similaire dans les sites pérennes et temporaires indique qu'une partie d'entre eux peut directement faire face à l'assèchement, par exemple en adaptant leur régime alimentaire pour se tourner vers les ressources d'origine terrestre (Hering and Plachter 1997, Paetzold *et al.* 2006). Une autre partie des invertébrés ripariens, en l'occurrence ceux collectés ni dans les sites pérennes ni dans les sites temporaires pendant la période d'assèchement, résiste vraisemblablement à l'assèchement par l'intermédiaire de stades d'hibernation ou de dormance synchronisés avec la période des assèchements (Uetz 1976, Lovei & Sunderland 1996). Les mécanismes de résilience sont certainement liés à la capacité de dispersion des espèces depuis les habitats pérennes. La migration des taxons depuis les sites pérennes par voie aérienne ou part dérive lors des crues et des remises en eau (Desender 1989, Bates *et al.* 2007, Corti & Datry 2012) peut permettre aux invertébrés ripariens de recoloniser les sites temporaires lorsque le cours d'eau est en eau. Pour les invertébrés qui restent actifs durant l'assèchement, les lits asséchés pourraient constituer des habitats favorables pour la recherche de nourriture, en procurant des proies facilement chassables aux prédateurs, des jeunes pousses de végétation aux phytophages ainsi que des graines ou des invertébrés aquatiques en voie de décomposition aux polyphages.

Les mécanismes de résistance et de résilience mis en évidence laissent penser que la période à laquelle les assèchements surviennent et l'accessibilité des refuges déterminent l'intensité des réponses des invertébrés ripariens. Les assèchements intervenant tôt dans la saison, c'est-à-dire avant que les invertébrés ripariens n'aient accompli leur cycle vital et qu'ils ne soient entrés dans un stade d'hibernation, diminueraient leurs capacités de résistance. De même, les assèchements localisés en amont des cours d'eau ne permettent pas la migration par dérive des espèces vers les sites temporaires et limiteraient la capacité de résilience des communautés lors des périodes en eau. La période des assèchements pourrait également avoir des répercussions importantes sur les nombreuses espèces rares et vulnérables qui vivent dans les zones ripariennes et plus particulièrement sur les bancs de graviers et bordure des cours d'eau (Eyre & Luff 2002, Andersen & Hanssen 2005).

La disparition temporaire de l'eau et des proies aquatiques lors de l'assèchement n'est pas un facteur limitant le développement des communautés d'invertébrés ripariens dans l'Albarine. Au contraire, la richesse taxonomique totale était plus élevée dans les sites temporaires que dans les sites pérennes. Etonnamment, ce résultat n'était pas dû à un plus grand remplacement d'espèces dans les sites temporaires, mais au fait qu'autant avant que pendant la période d'asséchement, la diversité dans les sites temporaires est supérieure à celle des sites pérennes. Les invertébrés ripariens pourraient contrebalancer, de par leur diversité et leur nombre, la disparition des proies aquatiques en servant de proies pour des consommateurs secondaires (oiseaux, batraciens, lézards, chauve-souris) qui utilisent les ressources aquatiques lors des périodes en eau.

Les fortes diversités et abondances observées dans les sites temporaires sont certainement révélatrices de l'intensité des liens trophiques entre les cours d'eau et leurs zones ripariennes. D'une part, en accord avec la partie 8.1.3., les zones ripariennes et les lits asséchés sont susceptibles de constituer des habitats complémentaires. Les ressources abandonnées par le cours d'eau lors de l'assèchement et la création de nouveaux habitats dans les lits asséchés pourraient se traduire par une augmentation de la diversité et de l'abondance des invertébrés ripariens. D'autre part, les invertébrés aquatiques des cours d'eau soutiennent les chaines alimentaires en impliquant plusieurs niveaux trophiques (Polis *et al.* 1997, Wesner 2012). Par exemple, les pics d'émergence des invertébrés aquatiques accroissent les populations d'oiseaux qui en retour vont exercer une pression plus importante sur les invertébrés terrestres lorsque les taux d'émergence des invertébrés aquatiques diminuent (Murakami and Nakano 2002). Dans les cours d'eau temporaires, les densités en invertébrés aquatiques sont faibles, de même que les taux d'émergence (Meyer & Meyer 2000, Bonada *et al.* 2007, Datry 2012). En conséquence, les populations d'oiseaux et *a fortiori* leur pression sur les invertébrés ripariens pourraient être réduites. Aussi, les communautés d'invertébrés ripariens dans les cours d'eau temporaires pourraient montrer une dépendance plus faible vis-à-vis des ressources aquatiques par rapport à ce qui est habituellement rapporté dans les cours d'eau pérennes (Hering and Plachter 1997, Paetzold *et al.* 2005), en raison d'interactions complexes entre différents niveaux trophiques.

8.1.4. La dynamique de la MOP dans les cours d'eau temporaires

Les cours d'eau temporaires sont des réacteurs biogéochimiques ponctués et longitudinaux

Larned *et al.* (2010) ont récemment développé, par analogie avec des études portant sur les sols en milieux arides, un modèle conceptuel sur la dynamique de la matière organique dans les C.E.T. L'idée centrale du modèle repose sur le fait que dans ce type de cours d'eau, les phases de stockage, de transport et de décomposition de la matière organique sont séparées dans le temps et dans l'espace. Ainsi, les fronts de remise en eau sont supposés entrainer dans des zones de dépôts situées à l'aval la matière organique accumulée sur les sédiments asséchés (Reid *et al.* 1998, Jacobson *et al.* 2000). Au sein des zones de dépôts, le retour de l'eau stimule les processus biogéochimiques qui interviennent dans la décomposition de la matière organique en composés organiques simples (Scherer *et al.* 1984). L'asséchement interrompt les processus qui s'opèrent en condition d'immersion, et amorce des processus tels que la photo-dégradation ou la décomposition par les organismes terrestres (Austin & Vivanco 2006, Collins *et al.* 2008). La remise en eau suivante transfère la matière organique ainsi transformée dans les zones de dépôts situées à l'aval. Elle rétablit ainsi les processus écologiques et biogéochimiques dépendants de l'eau. Les résultats de ces travaux de recherche amènent donc à considérer les C.E.T. comme des réacteurs biogéochimiques longitudinaux en raison des cycles répétés de transport, de stockage et de décomposition de la MO. Toutefois, les périodes en eau induisent des taux plus élevés pour la majorité des processus biogéochimiques par rapport aux assèchements. Ceci implique une transformation discontinue (ou ponctuée) de la matière organique. En définitive, la proportion de matière organique transformée augmente avec le nombre de cycles d'assèchement et de remise en eau.

Les résultats obtenus lors de ce travail de thèse soutiennent de manière générale le modèle développé par Larned *et al.* (2010) qui, jusqu'à présent, n'avait jamais été testé expérimentalement. Dans la rivière Albarine, il a été démontré que la remise en eau participe activement au transport vers l'aval de la MOP accumulée durant l'été et l'automne dans les lits asséchés. Les quantités soudainement mobilisées par le front de remise en eau sont très importantes. La concentration en MOP variant de 130 à 350 g/m^3 était près de 50 fois supérieure à celle des cours d'eau pérennes en crue (*e.g.* Bilby & Bisson 1992, Wallace *et al.* 1995). Elle présentait également une forte variabilité inter-sites suggérant la présence au sein du cours d'eau de zones de dépôts telles que des mouilles ou des méandres (Buffington *et al.* 2002, Jacobson & Jacobson 2012) où la MOP est temporairement stockée. Ainsi, les CET stockent et transportent la MOP par à-coups dont les amplitudes dépassent celles des cours d'eau pérennes.

Le caractère discontinu des processus biogéochimiques présenté dans le modèle de Larned *et al.* (2010) a également été confirmé lors de ce travail de thèse. En effet, dans la Selwyn River, le taux de décomposition de la MOP, sa colonisation par les invertébrés et l'activité microbienne diminuent avec l'augmentation de la durée totale des assèchements. La décomposition de la MOP dans le lit asséché était très faible mais non nul, certainement en raison de l'activité microbienne ou d'autres mécanismes tels que le lessivage des composés organiques simples (Taketa 1995), la photo-dégradation (Austin & Vivanco 2006) et la dégradation par les invertébrés terrestres. De plus, une expérience menée en parallèle de nos travaux a permis de montrer que le taux de décomposition dans les habitats aquatiques des C.E.T. diminuait avec la durée et la fréquence des assèchements précédents (Datry *et al.* 2011, **Annexe 1**). L'ensemble de ces résultats montre que plus un habitat présente de longues périodes d'assèchement, plus il accumule de matière organique lors des conditions terrestres et moins il est apte à soutenir les processus de décomposition.

Contrairement au modèle de Larned *et al.* (2010), nos résultats montrent que c'est la durée d'assèchement, et non leur fréquence, qui influence la décomposition de la MOP. Dans la Selwyn River, la fréquence des assèchements n'avait pas d'effet détectable sur le taux de décomposition de la MOP, sa colonisation par les invertébrés et l'activité microbienne, suggérant que cette dernière n'est pas stimulée par les cycles d'assèchement et de remise en eau, au même titre que dans les marais temporaires (Battle & Golladay 2001). Ainsi, il apparaît que les périodes de remise en eau peu fréquentes mais de longue durée affectent la décomposition de la MOP, alors que celles de courte durée mais très fréquentes ont un effet négligeable. La faible contribution des fronts de remise en eau à la recolonisation des habitats par les invertébrés aquatiques rapportée dans l'Albarine soutient l'idée selon laquelle des durées de remise en eau relativement importantes sont nécessaires pour stimuler les processus écologiques impliqués dans la décomposition de la MOP, notamment la recolonisation des habitats aquatiques par les invertébrés.

Implications à l'échelle des réseaux hydrographiques

À plus large échelle, la dynamique de la matière organique dans les C.E.T. pourrait avoir des répercussions sur les cours d'eau situés en aval, en influençant les quantités de nutriments utilisables par les organismes ainsi que les périodes où ils sont disponibles (Datry *et al. in review*). Ainsi, lorsque l'assèchement interrompt le transport de matière organique, la productivité des écosystèmes aquatiques situés en aval pourrait diminuer, en raison d'une forte baisse des ressources nutritives utilisables par les consommateurs primaires. Au contraire, les remises en eau provoquent un apport soudain et massif de matière organique et de nutriments susceptibles de stimuler en retour la productivité de l'écosystème en fournissant carbone et azote aux organismes hétérotrophes (Jacobson *et al.* 2000). Toutefois, des apports excessifs de matière organique et de nutriments pourraient aussi provoquer des phénomènes d'anoxie, lorsque la quantité d'oxygène consommée lors de la décomposition de la matière organique dépasse celle produite par la photosynthèse (Hladyz *et al.* 2011). Comme les cours d'eau en tête de bassin jouent un rôle prépondérant dans l'apport de matière organique aux cours d'eau situés en aval (Vannote *et al.* 1980, Wallace *et al.* 1995) et qu'ils sont aussi les plus enclins à subir des périodes d'assèchement (Lowe & Likens 2005), les conséquences des phénomènes présentés ci-dessus pourraient se répercuter sur l'ensemble d'un réseau hydrographique, des secteurs directement en aval d'un C.E.T. jusqu'aux estuaires.

8.1.5. Implications des résultats pour la gestion des cours d'eau

Malgré un nombre croissant d'études réalisées sur les C.E.T., il est encore difficile aujourd'hui de prendre en compte du rôle écologique des phases terrestres. Les résultats de nos travaux fournissent quelques pistes d'amélioration, qui demandent à être approfondies.

Tout d'abord, il est désormais acquis que les lits asséchés ne sont pas des habitats biologiquement inactifs. Ils sont des refuges pour les invertébrés aquatiques ayant la capacité de résister aux assèchements et contribuent ainsi au développement des communautés aquatiques lors des remises en eau (Datry *et al.* 2012). De plus, sur l'Albarine et l'Asse, plus de 130 taxons d'invertébrés terrestres ont été collectés dans les lits asséchés, avec une moyenne de 55 taxa par site. La comparaison de ces valeurs avec celles d'autres travaux dans les mêmes cours d'eau (Datry 2012) montre que la richesse taxonomique des invertébrés terrestres est deux fois supérieure à celle des invertébrés aquatiques. Par conséquent, les lits des cours d'eau temporaires présentent un intérêt pour la conservation de la biodiversité.

Les liens entre les communautés des lits asséchés et celles des zones ripariennes, mis en évidence par nos travaux, invitent à une prise en compte globale de la biodiversité de ces milieux. Si les zones ripariennes ne contiennent pas plus d'espèces que les habitats environnants, elles présentent toutefois des communautés spécifiques et notamment des espèces vivant uniquement en bordure des cours d'eau et dont certaines sont considérées comme menacées (Eyre & Luff 2002). En Angleterre par exemple, plus de 20% des carabes habitant les bancs de gravier des cours d'eau sont des espèces vulnérables ou en danger (Sadler *et al.* 2004). Ainsi, une partie des espèces inféodées aux zones ripariennes et susceptibles de coloniser les lits asséchés relèvent d'un statut de conservation particulier. Ce qui implique, en matière de gestion des cours d'eau et de préservation de ces espèces, de considérer également leur présence dans les lits asséchés.

Sur le plan fonctionnel, les invertébrés des lits asséchés interviennent certainement dans les chaînes trophiques, la production végétale et le recyclage des nutriments (Kellert 1993, Williams 1993). D'abord, parce qu'ils constituent une source de nourriture pour de nombreux prédateurs (*e.g.* oiseaux, lézards, chauves-souris, batraciens). Ensuite, parce que les espèces phytophages contribuent à réguler le développement de la végétation et à limiter la colonisation des lits asséchés par les plantes envahissantes qui sont souvent favorisée dans les milieux perturbés (MacDougall & Turkington 2005). Enfin, parce que les espèces détritivores, même si elles semblent peu nombreuses dans les lits asséchés, participent dans une certaine mesure au recyclage de la matière organique et à l'apport de nutriments.

Les cours d'eau temporaires sont soumis à des pressions anthropiques pouvant intervenir à la fois lors des phases aquatiques et terrestres. Nos travaux ont révélés des liens forts entre zones ripariennes et lits asséchés associés. Aussi, les activités humaines qui modifient les communautés ripariennes lors des périodes en eau vont probablement influencer la composition des assemblages d'invertébrés dans les lits asséchés. Par exemple, les coupes à blanc réduisent la capacité des zones ripariennes à maintenir les espèces qui leur sont spécifiques (Baker 2006, Rykken *et al.* 2007) et peuvent en retour limiter la capacité des invertébrés ripariens à coloniser les lits asséchés. De même, l'endiguement des cours d'eau et les éclusés réduisent le nombre et la taille des bancs de graviers, modifient leur organisation le long du cours d'eau et contribuent au colmatage du substrat avec, comme conséquence finale, une diminution de la diversité et de l'abondance des communautés d'invertébrés ripariens (Bates *et al.* 2007, Van Looy *et al.* 2007, Paetzold *et al.* 2008). En période d'assèchement, les activités de loisir (4x4, quads, motos) et l'extraction de sédiments utilisent souvent les lits des C.E.T. La destruction ou la modification d'un certain nombre de micro-habitas qu'il en résulte, peut conduire à une homogénéisation des lits asséchés et à une réduction de la diversité taxonomique des organismes qu'ils abritent (Steward *et al.* 2012). Enfin, comme le montrent les résultats de cette thèse, les invertébrés terrestres des zones ripariennes sont capables de résister à la raréfaction de la ressource en eau et des proies aquatiques, notamment au travers de traits d'histoire de vie synchronisés avec les périodes naturelles d'assèchement. Dans ces conditions, les activités humaines consommatrices d'eau, qui modifient significativement les dates moyennes et la durée des périodes d'assèchement naturelles, risquent d'impacter de manière négative les communautés d'invertébrés ripariens – voire les chaînes trophiques (Larned *et al.* 2010, Döll &.Müller Schmied 2012).

Sur le long terme, des recherches sont nécessaires pour comprendre comment les invertébrés terrestres des lits asséchés sont impactés par les perturbations naturelles ou d'origine anthropique. Pour cela, il est important de décrire les relations qu'entretiennent ces espèces avec les facteurs abiotiques, et de déterminer précisément les effets des cycles d'assèchement et de remise en eau sur la structure et la composition de leurs communautés (Steward *et al.* 2011). Ces recherches permettront de confirmer ou infirmer l'existence de liens entre les invertébrés terrestres et les perturbations d'origine anthropique. Mettre en évidence de tels liens permettrait d' envisager l'utilisation des invertébrés terrestres des lits asséchés comme des indicateurs biologiques de la qualité écologique des C.E.T. en phase d'assèchement

Enfin, les résultats des travaux de recherche montrent que les C.E.T. transportent de manière soudaine et temporaire des quantités très importantes de MOP. Si ce phénomène peut être bénéfique aux écosystèmes aquatiques situés en aval, il peut aussi conduire à des situations d'anoxie préjudiciables aux organismes aquatiques et la valeur économique de ces écosystèmes. En conséquence, la capacité des cours d'eau temporaires à exporter et stocker la matière organique au sein d'une multitude de patchs semble primordiale pour le fonctionnement des écosystèmes aquatiques situés en aval. Les perturbations d'origine anthropique qui réduisent la complexité du cours d'eau, tels que l'endiguement ou l'élimination des embâcles diminuent sa capacité de stockage de la MOP (Díez *et al.* 2000, Flores *et al.* 2011). Lorsque des cours d'eau temporaires sont présents dans les réseaux hydrographiques, l'absence de zones de stockage pourrait favoriser l'accumulation de quantités trop importantes de MOP dans les retenues d'eau ou dans les estuaires et provoquer des phénomènes d'anoxie (Hladyz *et al.* 2011). D'une manière plus générale, les effets de cycles d'assèchement et de remise en eau sur la dynamique de la MOP et les écosystèmes en aval pourraient être étendus au transport, au stockage et à l'accumulation des composés inorganiques et des polluants.

8.2. PERSPECTIVES

8.2.1. Influence de la position des assèchements sur les communautés ripariennes

Les connaissances acquises durant ce travail de thèse sur l'organisation des communautés d'invertébrés ont montré que les zones ripariennes des secteurs pérennes situées en amont sont une source de colonisateurs pour les zones ripariennes des secteurs temporaires et participent à la résilience de ces derniers. En effet, les différences de composition des communautés ripariennes entre secteurs pérennes et secteurs temporaires sont moins importantes avant que pendant les assèchements. Ce résultat laisse penser que les espèces qui disparaissent des secteurs temporaires pendant les assèchements, sont aussi capables de les recoloniser lors de la remise en eau depuis les secteurs pérennes situés en amont. Cette dispersion fait sans doute appel à la capacité des espèces à se déplacer le long des zones ripariennes, en volant ou par dérive au moment des épisodes de crue et de remise en eau.

Les assèchements peuvent survenir en amont, au milieu ou en aval des cours d'eau (Lake 2003). La position des secteurs temporaires pourrait donc avoir des conséquences sur la résilience des communautés d'invertébrés ripariens vis-à-vis des assèchements, en contrôlant l’existence et l’intensité des mécanismes de dispersion des espèces depuis les secteurs pérennes. Ainsi, lorsque les assèchements surviennent en tête de réseau, seuls les organismes capables de dispersion par voie aérienne peuvent migrer des secteurs pérennes vers les secteurs temporaires. En revanche, lorsque les assèchements surviennent en aval, tant la dérive dans le cours d’eau que la dispersion par voie aérienne sont susceptibles de favoriser la migration des individus. Enfin, lorsque les assèchements surviennent au milieu, les deux mécanismes s’opèrent mais l’intensité de la migration par voie aérienne pourrait être plus importante, en raison de migration depuis l’amont et l’aval. On peut donc s’attendre à ce que la différence de composition des communautés ripariennes entre les secteurs pérennes et temporaires d’un même cours d’eau soit plus importante lorsque les assèchements surviennent en tête de réseau qu’en aval ou au milieu des cours d’eau.

Pour tester ces prédictions, il s’agirait de sélectionner différents cours d’eau (n > 9) présentant des assèchements en amont, au milieu et en aval du réseau¸ puis d’échantillonner les communautés ripariennes, avant et pendant les assèchements, à l’aide de pièges Barber. Cette démarche permettrait ainsi de comparer les différences de structure et de composition des communautés entre les secteurs pérennes et temporaires, avant et pendant les assèchements en fonction de la position des assèchements au sein du cours d’eau.

L’influence de la position des assèchements sur la dispersion des espèces pourrait aussi être testée à l’échelle des populations, en considérant leur variabilité génétique dans les secteurs pérennes et temporaires. En effet, il se pourrait que les populations des secteurs temporaires soient plus isolées de celles des secteurs pérennes, quand les assèchements surviennent en tête de réseau que lorsqu’ils se produisent en aval avec, comme conséquence, une variabilité génétique plus faible. Cette hypothèse pourrait être testée sur deux espèces : l’une capable de voler, l’autre non, ce qui permettrait en outre de mieux appréhender le rôle de la dispersion par voie aérienne. Parmi les choix possibles, *Pardosa agricola* (Araneae) et certains Bembidion (Carabidae) présentent l’avantage d’être présents dans de nombreux cours d’eau de France. Des marqueurs génétiques sont déjà disponibles pour *Pardosa agricola* (Lambeets *et al.* 2010)

8.2.2. Interactions trophiques au sein des zones de transitions terrestre-aquatique

Les effets en cascade des assèchements sur les communautés ripariennes, notamment dus à la disparition des proies aquatiques, ont été étudiés de manière indirecte dans le cadre de cette thèse. Les résultats n'ont pas mis en évidence de diminution de la diversité ou de l'abondance des invertébrés ripariens prédateurs. D'autres types de proies sont donc disponibles en quantité suffisante. L'étude du régime alimentaire des invertébrés ripariens en périodes d'assèchement permettrait de mieux connaître les mécanismes de résistance aux assèchements et ainsi, mieux comprendre l'importance des flux terrestre-aquatique dans les cours d'eau.

Lors des assèchements, il est probable que les invertébrés prédateurs soient capables de modifier leur alimentation, en passant, par exemple, d'un régime alimentaire centré principalement sur les invertébrés aquatiques à un régime alimentaire composé essentiellement d'invertébrés terrestres (Hering & Plachter 1997, Paetzold *et al.* 2005). La comparaison des signatures isotopiques des invertébrés prédateurs serait un bon moyen de tester cette hypothèse. L'échantillonnage devra comprendre les invertébrés prédateurs provenant, à la fois de secteurs temporaires, avant et pendant les assèchements et de sites de référence pérennes, de manière à pouvoir dissocier l'effet des assèchements sur les variations saisonnières du régime alimentaire. Une première expérience basée sur les isotopes du carbone et de l'azote a été développée sur l'Albarine dans le cadre de ce travail de thèse. Mais les résultats n'ont mis en évidence aucune différence de rapport C/N entre les invertébrés terrestres et aquatiques et les litières de feuilles. Cela suggère que, dans l'ensemble, la matière organique autotrophe du cours d'eau contribuait peu au développement des chaînes trophiques. Les invertébrés utilisent plutôt celle d'origine terrestre. D'autres isotopes, comme l'hydrogène ou l'oxygène, doivent donc être utilisés en fonction du cours d'eau étudié (Hobson *et al.* 1999, McCluney & Sabo 2010)

Jusqu'à présent, les études menées sur les C.E.T. se sont toujours intéressées aux invertébrés aquatiques ou terrestres, sans jamais considérer les interactions biotiques entre ces deux composantes. Dans les plaines alluviales, il est désormais connu que les invertébrés aquatiques sont une ressource alimentaire non négligeable pour les invertébrés terrestres (Sanzone *et al.* 2003, Paetzold *et al.* 2005, Akamatsu & Toda 2011). Dans les C.E.T., les transitions spatiales mais aussi temporelles des conditions aquatiques vers des conditions terrestres et inversement pourraient être à l'origine d'interactions intenses entre invertébrés aquatiques et terrestres, *via* la prédation. Bien que totalement inconnu, cet aspect pourrait jouer un rôle important dans le fonctionnement écologique des C.E.T., en participant au transfert d'énergie et de nutriments entre les écosystèmes terrestre et aquatique.

Les interactions biotiques entre invertébrés terrestres et aquatiques pourraient être précisées par une expérimentation de terrain reposant sur un contrôle de l'accès des premiers aux seconds. L'expérimentation consisterait à répartir le long d'un front d'assèchement des exclos et des enclos permettant ou empêchant la prédation des invertébrés aquatiques, puis après collecte et dénombrement des individus en cours de dessiccation, à comparer la diversité taxonomique et les densités des invertébrés aquatiques en fonction de la prédation (possible ou impossible) et de la durée d'assèchement

8.2.3. Modélisation de la dynamique de la MOP

Les connaissances acquises sur la dynamique de la MOP ont montré qu'elle était très largement influencée par les cycles d'assèchement et de remise en eau. Les effets observés pourraient notamment se répercuter sur l'ensemble d'un réseau hydrographique. Afin de comprendre comment la dynamique de la matière organique est influencée par les assèchements à l'échelle d'un bassin versant, il conviendrait de réaliser des bilans pluriannuels d'apport et d'export de matière organique particulaire et dissoute, à l'aval de plusieurs cours d'eau temporaires et pérennes, dans différents réseaux hydrographiques. Les mesures obtenues permettraient de modéliser la dynamique de la matière organique ainsi que les flux de carbone (Acuña & Tockner 2010) à large échelle, et de simuler la dynamique de la matière organique sous différents scénarii de durées et de fréquences d'assèchements.

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ANNEXES

ANNEXE 1

Flow intermittence controls leaf litter breakdown in a French temporary alluvial river: the “ drying memory”.

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ABSTRACT

The inputs and breakdown of terrestrial leaf litter in streams is a fundamental ecological process that sustains in-stream foodwebs and secondary production. In temporary rivers, litter breakdown is reduced during dry phases, but the long-term effect of alternating drying and wetting cycles on litter breakdown is still poorly understood. We tested the hypothesis that leaf litter breakdown (LLB) in temporary rivers is primarily controlled by flow permanence (the number of flowing days over a given period expressed in %), and that drying events affect LLB during leaf fall periods through reduction of microbial activity and the modification of aquatic invertebrate assemblages. LLB rates (*k*), microbial activity and invertebrate assemblages were determined in winter at 10 cross-sections scattered along a flow permanence gradient on the temporary Albarine River, France. Results demonstrated that summer drying events affected the breakdown process for up to 6 months after flow has resumed in the river. LLB rates decreased exponentially with decreasing flow permanence, and with increasing drying event duration and frequency. These exponential relationships were observed for flow permanence variables calculated for the river for both 24-years and 1-year time periods prior to the experiment. A decrease in flow permanence from 100 % to 85 % led to a four-fold decrease in leaf litter breakdown rate. Microbial activity, which typically did not differ between cross-sections, failed to explain the between-cross-section differences in *k*. By contrast, invertebrate assemblages and, shredders, in particular, decreased exponentially with decreasing flow permanence and with increasing drying event duration and frequency.

Key-words: Intermittent river, drying events, ecological processes, microbial activity, invertebrate assemblages

INTRODUCTION

The most extreme form of hydrologic variability that characterizes many rivers consists of alternating wet and dry periods. Rivers that periodically cease to flow comprise a substantial proportion of the total number, length and discharge of the world's rivers (Tooth 2000). For instance, about 60% of total river length in the conterminous United States (National Hydrography Dataset, Nadeau and Rains 2007) is subject to dry periods. In addition, the number and length of temporary rivers may increase in many regions during the next century both due to climate and land-cover changes, as well as by the increasing freshwater abstraction for irrigation and other human uses (Larned *et al.* 2010a). Nevertheless, basic knowledge of temporary river ecology lags far behind that of perennial streams. Leaf litter breakdown (LLB), which is a fundamental ecological process in streams, has been the focus of > 800 studies in the last 30 years. However, less than 20 of these studies specifically concerned temporary rivers (from ISI Web of Science, March 2010). Consequently, breakdown mechanisms are poorly understood in temporary systems compared to permanent rivers and quantitative relationships between flow intermittence characteristics and LLB are still unexplored.

Drying timing, duration and frequency control many ecological processes and patterns in temporary wetlands and streams (Larned *et al.* 2010a). Wetland studies have reported faster LLB rates in temporarily inundated systems compared to permanent systems due to an increase in microbes, which enhanced palatability to invertebrates during subsequent flooding (Bärlocher *et al.* 1978; Ryder and Horwitz 1995). Others have found LLB rates to increase with the length of the wet period, which promotes leaching and creates more favorable conditions for microbes and invertebrates (Hietz 1984). By contrast, LLB is consistently slower in temporary streams than perennial systems (Herbst and Reice 1982; Boulton 1991; Pinna and Basset 2004). Short-term drying events immediately reduce breakdown processes in temporary streams, probably due to reduction in invertebrate density and richness (Boulton 1991; Maamri *et al.* 1997; Corti *et al. this issue*).

Whether drying events at different spatio-temporal scales have a long-term influence on LLB during flow periods in temporary streams remains unknown. Recently, it has been shown that long-term averaged flow permanence (proportion of time with flowing water) was an important driver of invertebrate biodiversity in temporary rivers. In particular, decreasing flow permanence reduces total and shredder invertebrate density and diversity in temporary rivers of New Zealand (Datry *et al.* 2007; Arscott *et al.* 2010) and UK (Stubbington *et al.* 2009). Moreover, drying event duration and frequency have been shown to reduce and modify microbial activity and diversity on streambeds (Amafiltano *et al.* 2007; Larned *et al.* 2007; Corti *et al. this issue*). Therefore, we expected summer drying events to persistently affect LLB during winter, once flow has recommenced. Measuring the persistent effects of summer drying events on autumn and winter LLB would represent an important step towards a better understanding of ecological functioning in temporary rivers.

In this study, we tested the hypothesis that LLB in a temporary river is influenced by flow permanence, and that summer and autumn drying events persistently affect LLB beyond leaf fall periods. We measured LLB rates during the flowing period starting in early winter, using *Alnus glutinosa* leaves, at 10 sites distributed on a gradient of flow permanence along the Albarine River, France. We also measured water chemistry, invertebrate assemblages and microbial activity at each site to assess the potential causal mechanisms of the breakdown process. We predicted that: i) summer drying events would influence winter LLB process, ii) flow permanence would alter microbial activity with higher microbial activity occuring when flow permanence is high, and iii) flow permanence would influence benthic invertebrate assemblages, and notably shredder density and richness, with higher shredder densities expected at higher flow permanence locations.

METHODS

Study sites

The Albarine River drains a 313 km^2 catchment in temperate eastern France (**Figure 1**). After flowing for 45 km on a karstic plateau and through gorges, the Albarine reaches a 15-km long alluvial plain and finally joins the Ain River. This alluvial plain is underlain by thick (> 36 m) glacio-fluvial deposits, the permeability of which ranges from 2 10^{-2} to 7 10^{-2} m s^{-1} (SIABVA 2000). The riparian vegetation along the plain is dense and dominated by *Alnus glutinosa*, *Salix* sp. and *Populus* sp.

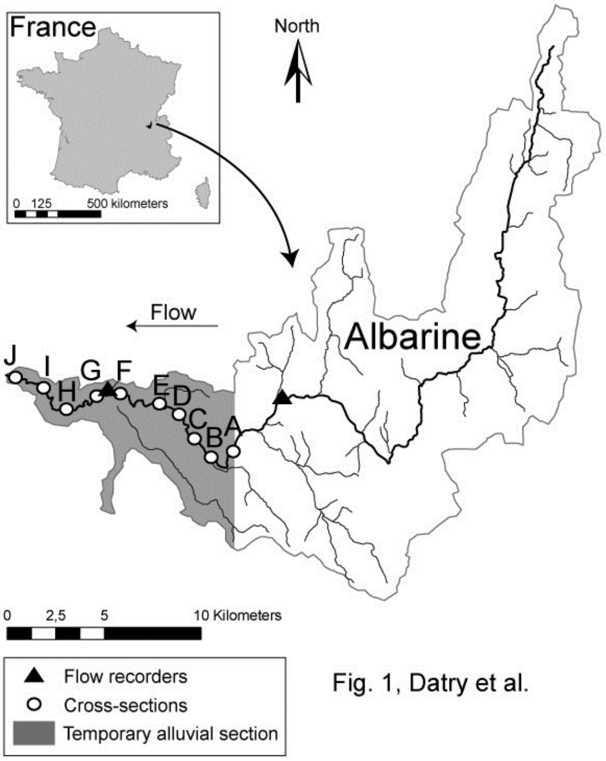

Fig. 1, Datry et al.

Figure 1. Map of the Albarine River catchment, eastern France, showing temporary and perennial reaches and positions of flow recorders. Capital letters indicate the location of the cross-sections used in the study.

Along the alluvial plain, the river is perched 1-14 m above the regional aquifer water table (Larned *et al.* 2010b) and continuous infiltration of surface water into the underneath aquifer leads to complete river section drying. Estimated surface water losses to the aquifer range from 0.85 to 2.5 m^3 s^{-1} (SIABVA 2000). As a consequence, the alluvial plain section is temporary and remains dry during summer and autumn (**Figure 1**). Flow resumption occurs generally at late autumn/early winter (Larned *et al.* 2010b). Two flow recorders have been measuring flow at daily intervals since January 1985 (http://www.hydro.eaufrance.fr/). One was located 4 km upstream from the temporary section (St Rambert en Bugey: mean river flow = 6.22 m^3 s^{-1};

average annual 7-day low flow = 0.22 $m^3 s^{-1}$), and another within it (St Denis en Bugey: mean river flow = 6.88 $m^3 s^{-1}$; average annual 7-day low flow = 0 $m^3 s^{-1}$) (**Figure 1**).

Hydrological modeling

In January 2008, 13 spot-gauging cross-sections were established at 0.3–3 km intervals in the alluvial plain section. The cross-sections were gauged at 2-4 week intervals from January 2008 to July 2009. Daily average flow at 500 m intervals along the alluvial plain section for the period 1 January 1985–21 April 2009 were estimated using a recently-developed hydrological model, ELFMOD (Rupp *et al.* 2008; Larned *et al.* 2010b). Briefly, ELFMOD uses regression analyses to estimate individual flow time-series at many cross-sections down the length of a river section. Input data consists of spot measurements of flow magnitude and flow state (flowing or dry) at multiple cross-sections, and time series of river flow at one or more sites along the modeled river section. The spot-gauging data are regressed on the flow data to produce a) regression parameters for estimating flow state and flow rate for each cross-section, on each date in the time series, and b) rates of flow loss or gain between consecutive cross-sections. The regression parameters are then used to estimate flow rates and confidence intervals at user-specified time-steps and distance intervals. The output from each ELFMOD run is a dataset of estimated flows arranged in a location x time matrix that corresponds to the spatial and temporal model domains. Model accuracy is evaluated and flow state misclassification rates determined using independent, validation datasets (Rupp *et al.* 2008) or by cross-validation (Larned *et al.* 2010b).

Flow time-series from the 2 recorders, and the 2008-2009 spot gauging data were used as input data. We calculated the following hydrological indices from the output reconstructed daily flow time series at each cross-section: i) flow permanence (FP), expressed as a %, and calculated as the number of flowing days over a given period; ii) average annual drying event frequency (N), expressed in number per year, and calculated as the average number of dry events per year; and iii) average annual drying duration (d), expressed in days, and calculated as the average duration of drying events and per year. These indices were calculated for the year preceding the field experiment (2008), and for the entire available flow time serie period (1985-2009), in order to test whether recent and long-term averaged intermittence statistics would show consistent relationships with actual LLB rates.

Field procedures

We used leaves of *Alnus glutinosa* because of its common abundance in the Albarine riparian vegetation. Freshly fallen leaves were collected just after abscission near Lyon, France, in October 2008 and kept dry in light-proof boxes. Petioles were removed from the leaves, which were dried (72 h, 105 °C), weighed into 4.6 ± 0.2 g portion, moistened (30 min.) and fastened into plastic-mesh-bags (15 x 15 cm ; mesh size: 6 mm). Litter bags were closed loosely with monofilament nylon line. Each bag was identified using a numbered plastic tag.

On the 17 February 2009, 150 litter bags were introduced into the stream (10 cross-sections scattered along the temporary section x 5 removal dates x 3 replicates). Riffles were used as the standard habitat at each cross-section (Young *et al.* 2008). Three control bags were retrieved just after installation at each cross-section (Date 1). Bags were then retrieved after 3 (Date 2), 8 (Date 3), 18 (Date 4) and 32 (Date 5) days of inundation (Abelho 2001). At each removal date, 3 bags per cross-section were randomly collected and returned to the laboratory in a cool box. No drying events occurred at any cross-section during the study period, and the last drying events had occurred > 31 days before the experiment started. Triplicate measures of water temperature, pH, dissolved O_2 (DO) and specific conductance were made for each removal date using field meters (WTW oxi330, WTW pH330 and WTW cond330, Weilheim, Germany).

Laboratory procedures

Two sets of three 5-mm leaf disks were cut from the leaves in each litter-bag with a cork borer. The first set of disks was used immediately to estimate microbial activity (see below) and the second was frozen for latter C/N analysis (see below). Materials remaining after removal of the disks were washed with tap water above a 63-µm mesh in order to eliminate biofilm and invertebrates from leaves. Leaf material was then dried (72 h, 105°C) and weighed. Invertebrates remaining on the sieve were preserved in 70 % ethanol for further sorting and identification (see below).

Leaf litter breakdown (LLB) rate

LLB rate (*k*) was calculated using the percent of original mass remaining at any date, following corrections made for the initial mass of each bag and the mass of leaf disks used for microbial and C/N analyses. *k* was calculated as the negative slope of a linear regression calculated from the natural logarithm of initial mass remaining as a function of time (Zar 1996). *k* was calculated for each cross-section by using 15 bags (3 bags x 5 dates). *k* was expressed on a degree-day basis in order to consider the influence of temperature (Minshall *et al.* 1983).

Microbial activity

Microbial activity in leaves was estimated using a fluorescein diacetate hydrolysis technique (FDA) adapted from Claret and Boulton (2003). This method measures non-specific esterase activities, and resulting data are strongly correlated with adenosine triphosphate (ATP) and cell-density estimates of microbial biomass (Stubberfield and Shaw 1990; Gillian and Duncan 2001). FDA has been thus widely used as a measure of microbial activity in soils (Aon & Colaneri 2001), river sediments (Claret and Boulton 2003; Datry and Larned 2008) or leaves fallen in streams (Imberger *et al.* 2008).

Sets of 3 leaf disks were immediately transferred to ashed glass vials (90 min, 550°C) with 3 ml of phosphate buffer (pH = 7.6) and 0.1 ml FDA solution. Vials were incubated (60-100 min) at room temperature (20°C) in darkness until a faint green color appeared. The reaction was stopped by adding 3 ml acetone. The supernatant was centrifuged (10 min; 4000 rev) and transferred to a test tube. Absorbance was measured at 490 nm with a Kontron instruments UVIKON 860 and converted to µmole of fluorescein. The leaf disks were dried (72 h; 105°C) and weighed. Microbial activity was expressed as µmole of FDA hydrolyzed per hour and per gram of leaf dry mass.

Leaf litter C/N

Sets of 3 frozen leaf disks were dried (72 h; 105 °C), transferred to tin containers (Thermo Fishers) and weighed. Nitrogen and carbon concentrations were determined using the "flash combustion" method (Verardo *et al.* 1990) on a FlashEA®1112 HT Elemental Analyser (Thermo Electron Corporation).

Invertebrate processing

Invertebrates removed from bags were counted and identified under a binocular microscope to genus for most of insects and to family or order level for other taxa. Invertebrates were later classified into functional feeding groups according to the groupings of Tachet *et al.* (2000). Densities were expressed as individuals per g of remaining leaf litter mass (individual.g^{-1} LL).

Data analysis

ANCOVAs and Scheffé post-hoc multiple comparisons were used to test for differences among cross-sections and over time in % initial mass remaining, physico-chemistry, C/N, FDA and invertebrate assemblage (i.e., taxonomic richness, total density, and shredder density), using triplicate values per date and cross-section.

Non-linear least squares regression models were used to examine relationships between intermittence variables and *k*. Linear regression models were used to examine relationships between *k* and physico-chemistry, C/N, FDA and invertebrate assemblage.

Data normality was tested by Shapiro-Wilks tests, and homogeneity of variances tested by mean of Bartlett tests. The % initial mass remaining at each date were arcsined-transformed and invertebrate densities were $\log_{10}(x+1)$-transformed prior to statistical analysis, which were performed using R software (http://cran.r-project.org/). The significance level for all statistical analyses was set at 0.01.

RESULTS

Temporal and spatial flow intermittence

FP decreased gradually with distance downstream along the alluvial section, with inputs by few karstic-fed small tributaries creating slight discontinuities (**Figure 2**). FP averaged over the 1985-2009 periods was generally lower than FP calculated for 2008 (**Table 1**). In 2008, FP ranged from 100 % (perennial) at the most upstream cross-section A, to 67 % at the most downstream cross-section J (**Figure 2, Table 1**). Along the study reach, drying frequency and duration increased steadily in the downstream direction (**Figure 2**). Drying frequency and duration were higher over the 1985-2009 period than for 2008 (**Table 1**). In 2008, drying frequency and duration increased from cross-sections A to J, from 0 to 12 and from 0 to 13.3 days, respectively (**Table 1**). A short decrease in dry period duration was observed at cross-section G, due to inflows from a small tributary (**Figure 2**).

Table 1: Intermittence statistics calculated for each cross-section along the study reach. Distances are given from cross-section A.

Cross-sections	Distance (km)	Flow permanence (%)		Annual drying frequency		Annual drying duration (days)	
		2008	1985-2009	2008	1985-2009	2008	1985-2009
A	0	100	99.8	0	0.2	0	3
B	1.4	100	94.7	0	1.7	0	11.4
C	2.5	100	98.2	0	0.9	0	7.2
D	3.5	100	98.2	0	1	0	6.9
E	5.3	97	82.9	2	4.3	6	14.3
F	8.3	87.7	73.5	3.5	5.7	13.3	17
G	10.0	88.4	72.9	4	5.5	8.4	18.1
H	13.2	77.9	64.8	11	7.5	7.2	17
I	14.2	76.6	63.3	11	8	7.7	16.8
J	14.6	66.7	58.7	12	8.8	9.8	17.1

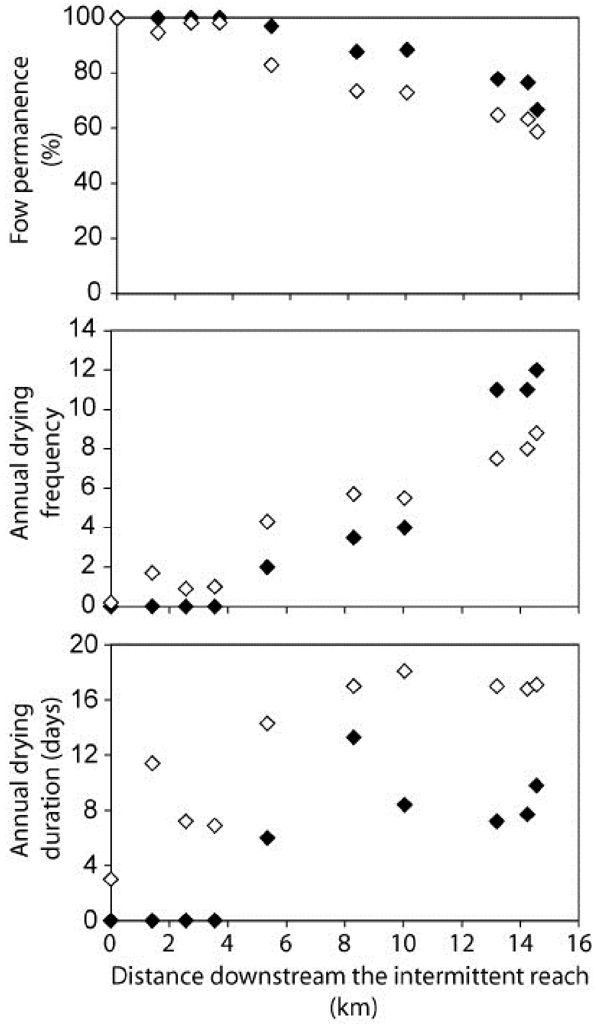

Figure 2. Longitudinal variations in flow permanence, average annual drying frequency, and average annual drying duration in the alluvial plain of the Albarine River, over the 1985-2009 period (open diamonds) and for 2008 (closed diamonds), based on ELFMOD outputs.

Temporal and spatial variation of leaf litter breakdown

Leaf litter mass loss increased exponentially over the study period at all cross-sections (**Figure 3**). However, temporal increase in mass loss strongly differed among cross-sections (ANCOVA, $p<0.0001$). As a result, *k* ranged from 0.0005 to 0.0115 over the 10 studied cross-sections. There was a general decrease in *k* from cross-section A to I, with an outlying value at cross-section D (**Table 2, Figure 3**). There was an abrupt decrease of *k* between A-F sections (>0.0028) and G-J sections (<0.0008).

Table 2: Breakdown rates (*k*) for each cross-section modeled from the Zar exponential model (Zar 1996), associated R^2 and p-values. *k* is expressed in degree-day (dd).* no leaf material remained at the last date, ** 2 bags were lost during the study period.

Cross-sections	Nb. Bags	*k*	R²	p-value
A	15	0.0059	0.80	<0.001
B	15	0.0073	0.72	<0.001
C	15	0.0046	0.34	<0.001
D	12*	0.0115	0.91	<0.001
E	15	0.0016	0.93	<0.001
F	14**	0.0028	0.65	<0.001
G	14**	0.0008	0.87	<0.001
H	15	0.0005	0.68	<0.001
I	15	0.0005	0.84	<0.001
J	15	0.0006	0.79	<0.001

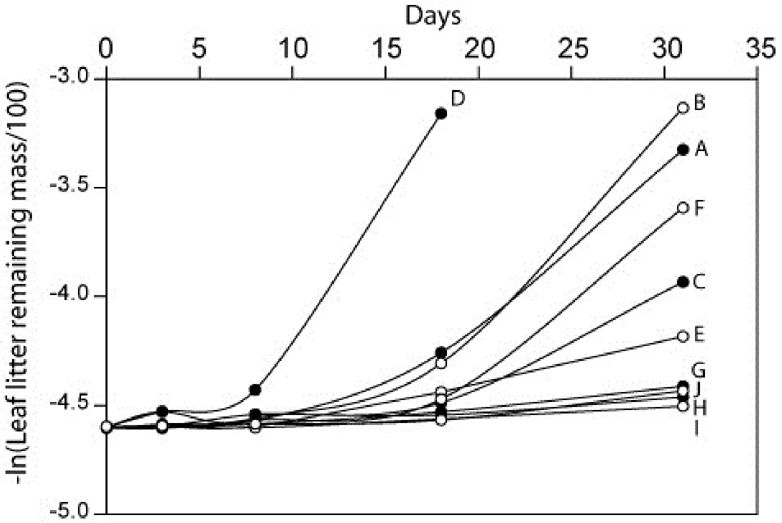

Figure 3. Temporal variation in % leaf litter remaining mass expressed in negative Neperian logarithm (Zar 1996), during the study period. Data are means ± 1 standard deviation (n=3).

Temporal and spatial variation in physico-chemistry, C/N, and FDA

Over the study period, temperature ranged from 4.5 to 9.1 °C (mean ± S D = 7.1 ± 1.2), pH from 8.3 to 8.5 (mean ± S D = 8.4 ± 0.1), DO from 8.4 to 13.7 mg.l^{-1} (mean ± S D = 11.6 ± 1.1), and specific conductance from 403 to 435 µS cm^{-1} (mean ± S D = 421 ± 16). All measured physico-chemical parameters varied during the study period (ANCOVA, **Table 3**). However, apart from specific conductance, which increased at all cross-sections, temporal variations were inconsistent across cross-sections (ANCOVA, **Table 3**). There was no difference in specific conductance among cross-sections, but significant differences in temperature, pH and DO (ANCOVA, **Table 3**).

Table 3. Differences in temperature, pH, dissolved oxygen (DO), specific conductance (Sp. Cond.), microbial activity (FDA), C/N ratios, total density, shredder density, taxonomic richness, between dates, cross-sections and dates by cross-sections. *P*-values in italics indicate significant results.

	Source of Variation								
	Dates			Cross-sections			Dates by Cross-sections		
	dl	F	*p*	dl	F	*p*	dl	F	*p*
Temperature	4	1707.24	*< 0.001*	9	248.41	*< 0.001*	36	19.91	*< 0.001*
pH	4	289.70	*< 0.001*	9	75.38	*< 0.001*	36	26.12	*< 0.001*
DO	4	417.65	*< 0.001*	9	22.17	*< 0.001*	36	7.29	*< 0.001*
Sp.Cond.	4	8.37	*< 0.001*	9	1.50	0.1567	36	1.31	0.1530
C/N	4	61.83	*< 0.001*	9	3.68	0.0676	36	1.12	0.7209
FDA	4	18.91	*< 0.001*	9	0.88	0.5414	36	1.25	0.1939
Total density	3	171.27	*< 0.001*	9	15.98	*< 0.001*	36	1.50	0.0816
Shredder density	3	19.27	*< 0.001*	9	125.38	*< 0.001*	36	0.92	0.4323
Taxonomic Richness	3	44.26	*< 0.001*	9	22.43	*< 0.001*	36	1.43	0.1142

There were consistent variations in C/N across cross-sections over the study period (ANCOVA, **Table 3**). C/N remained constant during the first 3 sampling dates, and then dropped slightly at 18 days and did not further vary over the study period (Scheffé tests). However, C/N was not different among cross-sections (ANCOVA, **Table 3**). FDA ranged from 0.08 to 2.68 µmol g^{-1} h^{-1} (mean ± S D = 0.54 ± 0.37). There were consistent variations in FDA across cross-sections over the study period (ANCOVA, **Table 3**). FDA decreased after the first day, and then remained relatively constant through the study period with a slight increase at 18 days (Scheffé tests). There were no differences in microbial activity among cross-sections (ANCOVA, **Table 3**).

Invertebrate assemblages

More than 30180 invertebrates from 51 taxa were collected from leaf litter bags (**Table 4**). The mean density was 116 invertebrates per g of leaf litter (range: 2–1 541, *n*=115). Chironomidae, Simuliidae and small Ephemeroptera instar were the 3 most abundant and frequent taxa, with respectively 9154, 1038 and 1020 individual g^{-1} LL and a frequency of occurrence of 99.1, 94.8 and 91.4 %, respectively (**Table 4**). Shredders accounted for 23 of 51 taxa, but they represented less than 8 % of the total number of invertebrates. Other important feeding groups were grazers and predators (**Table 4**). Taxa classified as both grazers and shredders were accounted for shredders.

Invertebrate taxonomic richness, total density and shredder density increased with time at all cross-sections (**Figure 4, Table 3**). These significant increases were very consistent among cross-sections (**Figure 4, Table 3**). Figure 5 shows temporal variations in taxonomic richness, total density and shredder density during the study period for 5 randomly-selected cross-sections along the FP gradient only. Increases in taxonomic richness and shredder density were relatively steady over time for each cross-section, while total density increased abruptly after 18 days (**Figure 4**). Apart from taxonomic richness whose spatial pattern remained constant over time, differences among cross-sections were gradually increasing over the study period, cross-section differences being the highest after 32 days (**Figure 4**). For instance, shredder density increased from 0.1 ± 0.1 to 1.2 ± 0.2 individuals g^{-1} LL between the first and the last sampling dates at cross-section J, whereas density rose from 2.7 ± 0.5 to 29.9 ± 7.3 individuals g^{-1} LL at cross-section A.

Table 4. Mean, minimum and maximum density per g LL^{-1}, feeding groups and frequency of occurrence (FO) of aquatic invertebrates. Shr: shredder; Grz: grazer; Dep feed: deposit feeder; Filtr: filterer; Pred: predator (s.l.); Para: parasite; Per: piercer; -: indetermined feeding group.

Taxon		Mean	Min - Max	Feeding groups	FO (%)
Ephemeroptera	*Baetis* sp.	2.8	0 – 60.5	Graz, Dep feed	77.6
	Caenis sp.	0.1	0 – 5.2	Dep feed, Shr	8.6
	Ecdyonurus sp.	0	0 – 0.2	Graz, Shr	0.9
	Electrogena sp.	0	0 – 2.6	Graz	4.3
	Epeorus sp.	0	0 – 0.5	Graz	3.4
	Ephemerella sp.	0.2	0 – 6.2	Shr, Graz	21.6
	Habroleptoides sp.	1	0 – 7.5	Graz, Shr	56
	Indetermined	8.9	0 – 112.8	-	68.1
	Rhithrogena sp.	0	0 – 0.5	Graz	4.3
	Torleya major	0.2	0 - 9	Graz	17.2
Plecoptera	*Brachyptera* sp.	0	0 – 0.5	Graz, Shr	6
	Isoperla sp.	0	0 – 1.7	Shr	6.9
	Leuctra sp.	2	0 – 12.8	Shr	83.6
	Nemoura sp.	0	0 – 0.7	Shr	5.2
	Indetermined	0	0 – 0.9	-	0.9
	Rhabdiopterix sp.	0	0 – 0.3	Shr	1.7
Trichoptera	*Allogamus* sp.	0	0 – 0.2	Shr, Graz, Pred	0.9
	Hydropsyche sp.	0.6	0 – 20.2	Filtr	31
	Hydroptila sp.	0	0 – 0.3	Pier, Dep feed, Shr, Graz	1.7
	Lepidostoma sp.	0	0 – 0.3	Shr	0.9
	Limnephilinae	0	0 – 0.2	Shr, Graz,Pred	0.9
	Rhyacophila sp.	0.5	0 – 16.1	Pred	37.9
	Sericostoma sp.	2.7	0 – 49.8	Shr	40.5
	Wormaldia sp.	0	0 – 0.3	Filtr, Graz	0.9
Diptera	*Atherix* sp.	0.1	0 – 2.3	Pred	22.4
	Ceratopogoninae	0.3	0 – 4.9	Pred, Shr, Dep feed	30.2
	Chironomidae	79.6	1.4 – 1215.5	-	99.1
	Clinocerinae	0	0 – 0.5	Pred	2.6
	Empididae	0	0 – 0.3	-	0.9
	Hemerodromiinae	0	0 – 1.1	Pred	3.4
	Limoniidae	0.1	0 – 7	Shr	4.3
	Simuliidae	9	0 – 108.9	Filtr	94.8
	Stratiomyidae	0	0 – 0.3	Shr, Graz, Dep feed	0.9
	Tipulidae	0	0 – 0.3	Shr, Dep feed, Pred	0.9
Coleoptera	*Elmis* sp.	0.2	0 – 4.5	Graz, Shr	24.1
	Esolus sp.	0	0 – 1.3	Graz, Shr	3.4
	Riolus sp.	0	0 – 0.5	Graz, Shred	0.9
Crustacea	Copepoda	0.4	0 – 4	-	44
	Gammarus sp.	0.6	0 – 6.3	Shr	44.8
	Isopoda	0	0 – 0.5	-	6
	Niphargidae	0	0 – 0.3	-	0.9
	Ostracoda	0.3	0 – 3.9	-	37.9
Oligocheta	Indetermined	4.7	0 – 38.9	-	91.4
Arachnida	Hydracarina	0.6	0 – 14.8	Shr	36.2
Planaires	*Dugesia* sp.	0	0 – 0.3	-	1.7
	Polycelis nigra-tenuis	0	0 – 0.5	Pred	6.9
Acheta	Erpobdellidae	0	0 – 0.5	Pred	3.4
	Glossiphonia sp.	0	0 – 0.5	Pred	5.2
	Haemanteria costata	0	0 – 0.2	Pier, Para	0.9
	Piscicola geometra	0	0 – 0.5	Para	0.9
Gasteropoda	Indetermined	0	0 – 2.7	-	1.7

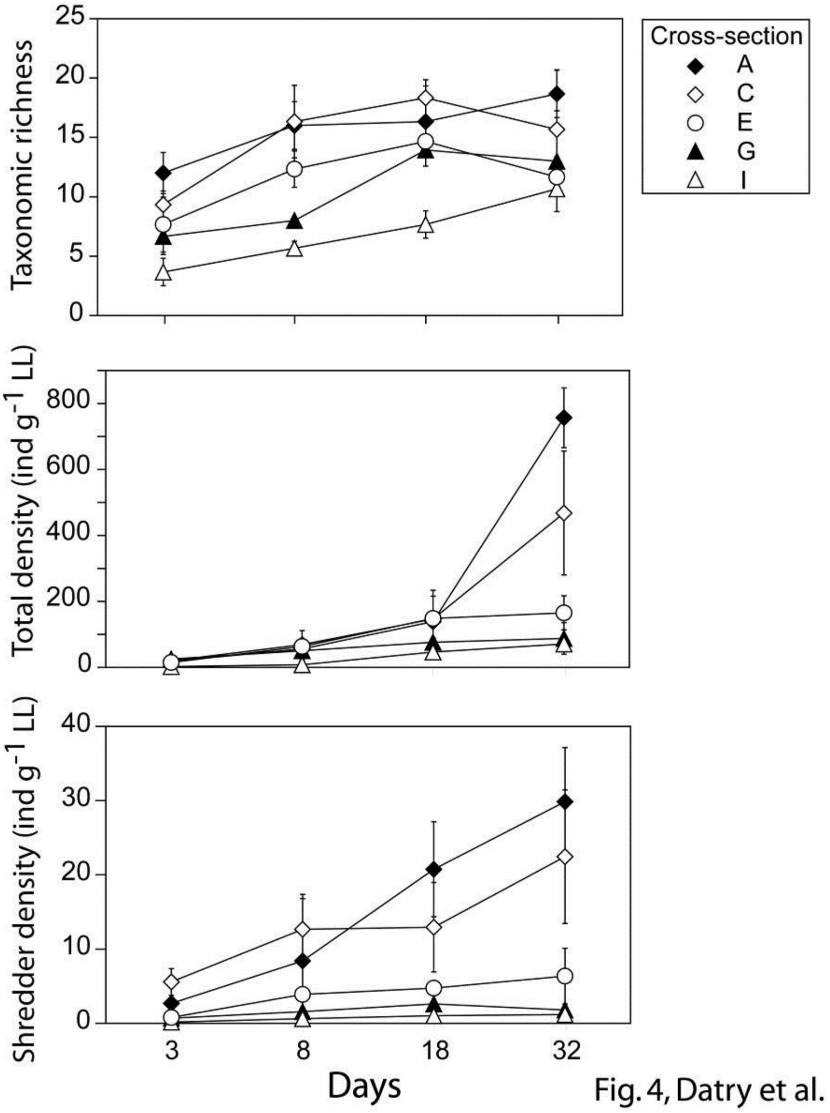

Figure 4. Temporal changes in taxonomic richness, total density and shredder density of invertebrate assemblages from litter bags of 5 selected cross-sections dispatched along the alluvial plain of the Albarine. Data are means ± 1 standard deviation (n=3).

Relationships between *k* and measured variables

LLB rate was related to intermittence statistics. Non-linear least squares regression models showed that *k* increased exponentially with increasing FP and decreased exponentially with increasing N and d for the 2 periods (2008 and 1985-2009) (**Figure 5**). There were no relationships between *k* and pH (R^2=0.01, *p*=0.901), dissolved oxygen (DO) (R^2=0.48, *p*=0.025) nor specific conductance (R^2=0.03, *p*=0.623). However, *k* tended to decrease slightly with increasing DO and temperature, as both variables increased continuously with increasing distance downstream. No relationships were detected between *k* and C/N (R^2=0.15 *p*=0.274) nor FDA (R^2=0.02, *p*=0.722).

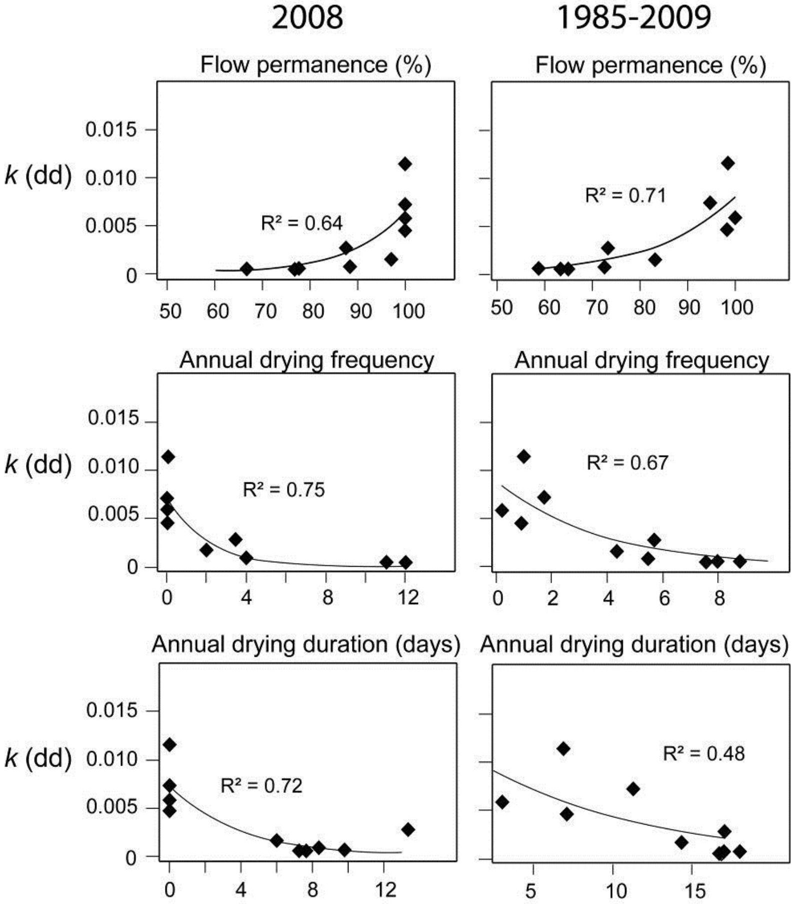

Figure 5. Relationships between LLB rates (*k*) and flow permanence (FP), average annual drying frequency (N) and average annual drying duration (d) for the 2 periods (1985-2009 and 2008). The lines represent the fit to the non-least squared regression model.

There were no relationships between *k* and invertebrate taxonomic richness, nor total density, but *k* increased linearly with shredder density (**Figure 6**). The absence of relationships between either taxonomic richness or total density was caused by an outlying point (cross-section D), which had higher *k* and shredder density than any other cross-section (see **Table 2**). Removing this point resulted in significant relationships between *k* and invertebrate taxonomic richness, and total density (R^2=0.70, and R^2=0.95, respectively). However, we did not remove cross-section D from our dataset, because we considered its "outlying behavior" due to a particularly high shredder density (**Figure 6**). The *k* ~ shredder density relationship indicated that an increase of 100 % in shredder density led to a 2 fold increase in *k*.

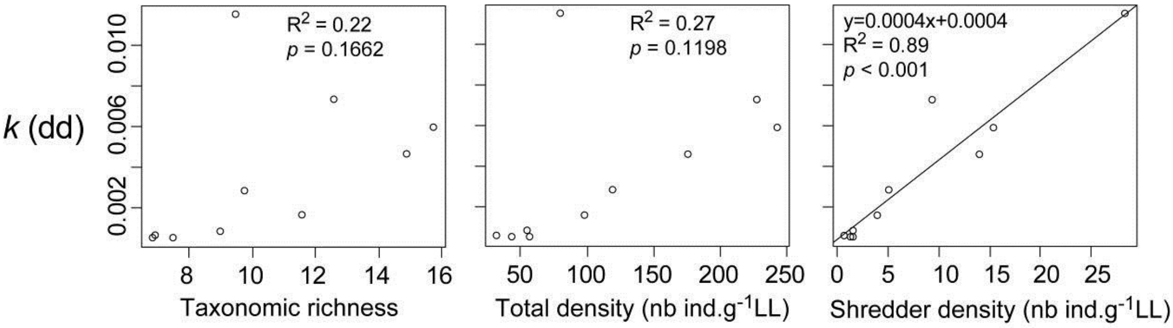

Figure 6. Relationships between LLB rates (*k*) and taxonomic richness, total density and shredder density of invertebrates assemblages from litter bags. All data are mean across dates (n = 9 to 12). The line represents the fit to the linear model.

Shredder density was strongly related to flow intermittence (**Figure 7**). Shredder density increased exponentially with FP, but exponential relationships were stronger for FP averaged over the 1985-2009 period (R^2=0.75) than for the year 2008 (R^2=0.65). Shredder density decreased exponentially with increasing frequency of dry events per year, whatever the period considered (**Figure 7**). Shredder density slightly decreased with average duration of dry events per year in the two periods considered **(Figure 7**).

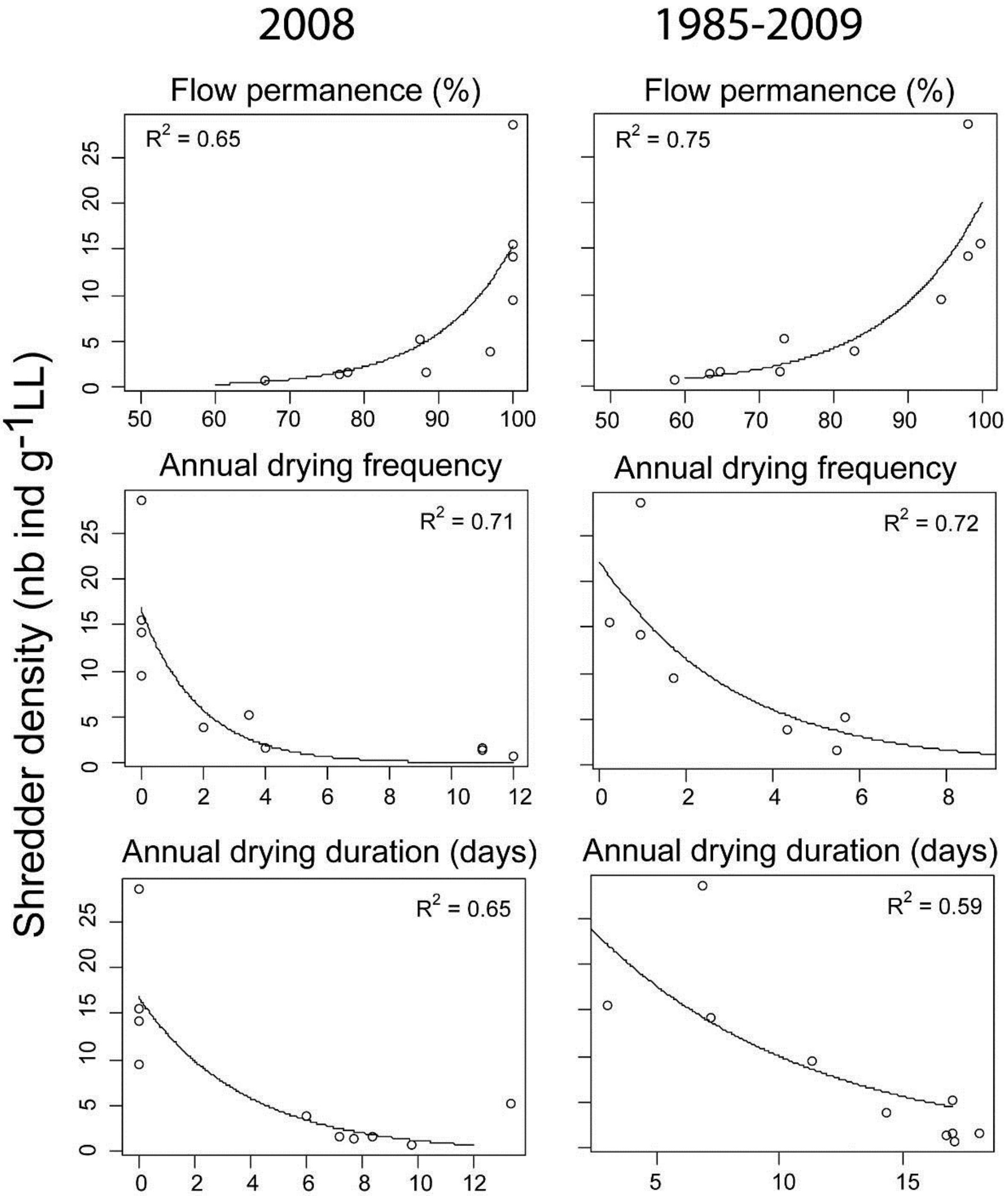

Figure 7. Relationships between shredder density of invertebrates assemblages from litter bags and flow permanence (FP), average annual drying frequency (N) and average annual drying duration (d) for the 2 periods (1985-2009 and 2008). All data are mean across dates (n = 9 to 12). The lines represent the fit to the non-least squared regression model.

DISCUSSION

Memory of drying: leaf litter breakdown and flow intermittence

Leaves falling into dry streambeds decompose much more slowly than in flowing streams (*e.g.* Kirby *et al.* 1983; Tate and Gurtz 1986; Boulton 1991; Maamri *et al.* 1997). However, many streams and rivers show strong seasonal drying patterns, drying events occurring during summer, and flow resumption during late autumn and early winter, coinciding hereby with the heaviest leaf fall. Our first prediction that summer drying events influence *k* during following flowing periods was largely supported by our results. Flow permanence (FP) had a dramatic influence on *k*, which increased very slightly with FP from 60 to 85% and then rose sharply from 85 to 100%. This influence was observed for the 2 periods considered, 1985-2009 and year 2008 alone. Similarly, the increased annual drying frequency (N) and duration (d) for the 2 periods slowed litter breakdown, and the relations were clearly not linear. Because breakdown rates were measured at least 31 days after flow resumption in the Albarine River, these results suggest that temporary streams remain persistently affected by drying events that have occurred throughout the previous summer season. Drying events not only strongly reduce breakdown processe when they occur in streams (Herbst and Geice 1982; Tate and Gurtz 1986; Boulton 1991; Corti *et al. this issue*), but also affect persistently leaf litter breakdown process long after flow has resumed during late autumn and winter. Since the Albarine River presents a very seasonal drying pattern, with summer drying and flow resumption in late autumn or winter, and moderate inter-annual variations in the frequency and duration of high flows (Larned *et al.* 2010b), it seems reasonable that relationships between intermittence indices and *k* observed for a particular year hold when averaging these indices over longer periods. These preceding results have strong implications for our full appreciation of the effects of flow regime on ecosystem processes in temporary rivers.

Differences in breakdown rates between temporary and permanent rivers have been reported previously, but to our knowledge, our study is the first that quantified the significance of flow permanence, drying frequency and duration on LLB in an intermittent river (but see Corti *et al. this issue*). Breakdown rates were reported previously to be 2 to 5-fold lower in temporary streams compared to perennial streams in Israel (Herbst and Geice 1982), Australia (Boulton 1991), Morocco (Maamri *et al.* 1997), Italy (Pinna and Basset 2004), and USA (Kirby *et al.*

1983). The breakdown rate of *Alnus glutinosa* in our uppermost, perennial cross-section A was similar to those reported for perennial streams in France (*e.g.* Gessner and Chauvet 1994, Lecerf *et al.* 1998). However, this rate was 10-fold higher than the most downstream (km 14) and most temporary cross-section J, and 5-fold higher that at cross-section E, which was located in the middle of the intermittence gradient (km 5). These strong differences in *k* within the same river system at relatively small distances underline the need to quantify flow intermittence and shifting from qualitative to more quantitative perspectives when considering temporary streams and rivers.

Greater understanding of intermittence~ecological processes are needed to predict the consequences of future changes in flow intermittence, which may result from changes in precipitation, runoff, aquifer storage and water abstraction/diversion (Strange *et al.* 1999; Larned *et al.* 2010a). *k*-FP relationships found in the Albarine River were typically exponential, and this suggests the existence of important thresholds at which breakdown is almost zero. This pattern indicates that very small changes in flow permanence, through change in either drying frequency or duration, would significantly reduce organic matter breakdown in temporary rivers. The existence of such thresholds could explain the very high variability in breakdown rates reported in the literature from temporary systems (*e.g.* Kirby *et al.* 1983; Boulton 1991; Maamri *et al.* 1997). In a context of climate change, we contend that FP represents a powerful hydrological variable to predict ecological processes such as leaf litter breakdown in temporary streams. The quantitative relationships between intermittence and LLB presented in this study were obtained on a single river, and quantitative relationships between intermittence and organic matter breakdown in rivers worldwide should confirm the applicability of our findings.

Drivers of leaf litter breakdown in temporary rivers

Our second prediction that FP alters microbial activity was not supported. Organic matter quality (measured as C/N) and potential microbial activity (estimated by FDA hydrolysis) did not vary along the FP gradient in the Albarine River. Neither did FDA and C/N vary consistently in time. Two pulses of microbial activity occurred during the study period, one immediately after incubation in the river, and another at t=18 days. Both could be a response to inputs of nutrients, especially dissolved and particulate carbon (Claret & Boulton 2003).

Discharge was relatively constant during this period, but increased slightly during the last 2 weeks of the experiment. Shifts from dry to wet conditions and associated leaching, and a slightly increase in discharge could have temporarily stimulated microbial activity on leaves through nutrient supply (Baldwin and Mitchell 2000). Shifts from dry to wet conditions have been reported to trigger biogeochemical processes in arid environments (McIntyre *et al.* 2009) and in a temporary wetlands (Barlöcher 1998). However, such triggers have not been observed in temporary rivers yet (Boulton 1991; Langhans and Tockner 2006, Corti *et al. this issue*).

Whereas several studies reported FDA values from temporary river streambed sediments (*e.g.* Claret and Boulton 2003; Datry and Larned 2008), only few FDA measures on leaf litter have been published. The range of microbial activity measured in the Albarine River was slightly above this reported by Imberger *et al.* (2008), who studied breakdown processes in southern Australian urban streams and suggested microbial activity to accelerate leaf litter breakdown in urban streams. Nevertheless, *k* do not correlate with microbial activity nor organic matter quality in the Albarine River, and we found microbial activity was not an important driver of leaf litter breakdown. However, this outcome could be put into perspectives: i) by the coarse resolution of FDA as a measure of microbial activity, ii) by the fact we did not measure fungal activity, iii) by the study period since winter-early spring is a low-temperature period and microbial assemblages are less active, and iv) by an overwhelming action of shredders in temporary rivers in leaf litter breakdown. Recent work highlighted the role of micro-organisms and fungi in leaf litter breakdown (Gessner and Chauvet 1994; Hieber and Gessner 2002; Gulis & Suberkropp 2003), but we did not measure specific enzymatic activity (*e.g.* xylosidase and glucosidase involved in cellulose degradation) or ergosterol content that could be used to assess more precisely the role of bacteria and fungi. Distributions of fungi and bacteria along FP gradients have never been reported to date in temporary rivers and would definitively deserve more research.

In the Albarine River, shredders seem to be the main driver of leaf litter breakdown and this driver was clearly influenced by flow intermittence. Temporal variations of physico-chemical variables during the study period do not follow a distinctive trend among all cross-sections. Although temperature and DO showed slight longitudinal variations, these variations were contrary to variations in *k*. By contrast, we found that invertebrates were influenced by the frequency and duration of drying events and overall flow permanence, as reported from New

Zealand (Datry *et al.* 2007; Arscott *et al.* 2010) and UK (Stubbington *et al.* 2009) rivers. Shredders density dropped dramatically with a two-fold decrease after FP slightly decreased from 100 to 90 %, and were virtually absent in the most temporary cross-sections. Previous studies have noted that shredders were both sensitive and intolerant to dessication and hence less abundant in temporary streams compared to perennial rivers (Williams *et al.* 2006). In fact, despite shredders represented only 8% of total density in the Albarine River, they appear to be the primary driver of leaf breakdown.

In winter, after flow had resumed in the river between 1 to 6 months depending on cross-sections, persistent differences in invertebrate assemblage found in leaf litter bags kept prevailing among cross-sections. This suggests that drying events persistently alter the composition of invertebrate assemblages in temporary rivers. Recolonisation by aquatic invertebrates of regularly drying segments in temporary rivers is a surprisingly fast process that has been highlighted previously (Miller and Golladay 1996; Gasith and Resh 1999; Williams 2006). This was ascribed to mechanisms developped by taxa to survive in dry riverbeds, including physiological, behavioural and morphological adaptations and to the presence of nearby refugia during dry periods. In the Albarine, upstream sections (A-D) remained perennial during the dry season in 2008 and no strong longitudinal variation in shredder density was observed. Therefore, these sections could be an important source of colonists after flow has resumed in the downstream temporary sections. Whereas recovery of assemblage composition to before drying levels occured rapidly after rewetting at the studied cross-sections (Datry, unpublished data), persistent differences in shredder density among cross-sections prevailed long after flow resumption. Moreover, shredder density showed exponential relationships with annual and interannual FP, thereby suggesting that drift was not a significant mechanism for recolonisation. Overall, this result suggests that even after long flowing periods, temporary streams cannot be viewed and managed simply as perennial streams, because of this “drying memory”.

Interesting questions are raised by our results concerning the ecological functioning of temporary streams, and the fate of leaves in the most temporary cross-sections. Because of an almost zero breakdown rate at cross-sections with FP lower than 75-80 %, leaves may accumulate in the riverbed both during dry periods and flowing periods without being decomposed. Spring floods may flush these stocks of organic matter, but the ecological consequences of such pulses are still unknown. Larned *et al.* (2010a) proposed a conceptual model of the biogeochemical functioning of temporary rivers. Advancing fronts transfer nutrients and organic matter to “reservoirs” downstream. These reservoirs may be pools, bar tops, or other sites where material is retained during dry periods. At these sites, the temporary presence of water may stimulate some biogeochemical and ecological activity (Larned *et al.* 2010a; Corti *et al. this issue*). However, in the Albarine River, leaf breakdown process rate still remained very low during flowing periods at intermittent cross-sections. Drying causes the cessation of many water-dependent processes, and the onset or intensification of processes such as photodegradation, dehydration, fungal breakdown and comminution by terrestrial invertebrates (Austin & Vivanco 2006; Collins *et al.*, 2008). The fate of leaves fallen in the Albarine riverbed during dry periods remains unknown and more research is need to understand processes occuring during dry phases of temporary river systems.

Sources of organic matter in the most temporary cross-sections of the Albarine may be distinct from those in the perennial section. Leaf litter breakdown is assumed to be a fundamental process through which an aquatic system is supplied in matter and energy by inputs of terrestrial material (*e.g.* Webster *et al.* 1999; Cummins 2002). At sites along temporary rivers where breakdown is reduced both during dry and flowing periods, organic matter may be supplied by inputs from upstream perennial sites. In turn, these shifts in organic matter supply could strongly affect stream foodweb structure and dynamic in temporary sections and could represent an additional mechanism by which flow cessation affects biodiversity in temporary rivers.

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ANNEXE 2

Spatial and temporal aquatic-terrestrial transitions in the temporary Albarine River, France: responses of invertebrates to experimental rewetting.

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SUMMARY

In temporary rivers, viewed as coupled terrestrial-aquatic ecosystems, spatial and temporal transition zones between aquatic and terrestrial conditions are common and occur simultaneously. The effects of artificial rewetting on terrestrial and aquatic invertebrate assemblages were examined in dry sediments collected from the Albarine River, France. Rewetted sediments had previously been dry for between 0.1 and 142 days. Dry sediments were collected directly from the streambed (DS) and from riparian gravel bars (RGB). We first predicted that invertebrate responses to rewetting would vary with the duration of the preceding dry period. Second, we predicted convergence of the invertebrate assemblages in DS and RGB sediments with increasing duration of the dry period. Third, we predicted that an aquatic “invertebrate seedbank” (aquatic life stages that persist within streambed sediments during dry periods) would contribute substantially to the resilience of benthic assemblages. Results indicated that the duration of the dry period was the primary driver of aquatic and terrestrial responses to artificial rewetting. The density and richness of aquatic taxa decreased with the duration of the dry period in both DS and RGB sediments, whereas the density of terrestrial invertebrates increased in DS sediments. No convergence between DS and RGB assemblage composition was observed with an increasing dry period. Although there were more aquatic organisms in DS sediments than in RGB sediments, there was no difference in taxonomic richness between sediment types. Even after prolonged dry periods (142 days), there was typically a lower density and taxonomic richness of terrestrial invertebrates in DS sediments than in adjacent RGB sediments. The results suggest that the aquatic invertebrate seedbank could contribute substantially to the resilience of benthic assemblages in the Albarine River, in addition to other mechanisms such as drift and oviposition. Of the taxa in the benthos before and after the summer dry period, 65% were also recovered from artificially rewetted DS sediments. The simultaneous presence of temporal and spatial terrestrial-aquatic transition zones in temporary rivers increases successional diversity (i.e. mosaics of dry and saturated streambed patches at various stages of terrestrial and aquatic succession). This contribution to biodiversity emphasizes the need to protect dry reaches of temporary rivers.

Key-words: invertebrate seedbank, ecotones, ephemeral river, flow intermittence, dry events, resilience

INTRODUCTION

Ecotones have been defined spatially as narrow transition zones between dissimilar environments (Naiman & Decamps, 1997), and temporally as short transitional periods between persistent and dissimilar states (Pinay *et al.*, 1990; Larned, Datry & Robinson, 2007). Processes occurring along these transition zones and over varying temporal resolutions influence the long-term dynamics of communities and ecosystems (Naiman, Decamps & Pollock, 1993; Ward, Tockner & Schiemer, 1999). In temporary rivers, which can be viewed as coupled terrestrial-aquatic ecosystems (Larned *et al.*, 2010), spatial and temporal transition zones between aquatic and terrestrial conditions are common and occur simultaneously.

In natural rivers, fringing riparian zones (*e.g.* protruding gravel bars and banks) constitute spatial transition zones between aquatic and terrestrial conditions and have high biodiversity (Gregory *et al.*, 1991; Naiman & Décamps, 1997; Ward & Tockner, 2001; Tockner & Stanford, 2002; Paetzold, Schubert & Tockner, 2005). In particular, riparian zones are inhabited by a diverse terrestrial invertebrate fauna including spiders, rove beetles, ground beetles and ants (Hering & Plachter, 1997; Manderbach & Hering, 2001; Sadler, Bell & Fowles, 2004; Paetzold *et al.*, 2005). Several of these taxa are predatory (*e.g.* lycosid spiders, carabid beetles) and their diet includes aquatic invertebrates inhabiting the adjacent stream channel (Hering & Plachter, 1997; Paetzold *et al.*, 2005; Lambeets *et al.*, 2008; Greenwood & McIntosh, 2010). During dry phases in temporary streams, riparian zones gradually become part of the dry riverbed. As a consequence, the terrestrial predators inhabiting riparian gravel bars may decrease as the duration of the dry period increases.

Alternating wet and dry periods in temporary rivers constitute temporal transition zones (Larned *et al.*, 2010; Datry, Corti & Philippe, 2011). When surface water disappears, riverbed sediments shift rapidly from aquatic to terrestrial conditions. Consequently, the invertebrate assemblage shifts from one characteristic of flowing waters to one typical of a dry riverbed (Larned *et al.*, 2007). These changes relate firstly to taxon-specific responses to desiccation. Some desiccation-sensitive aquatic taxa die within a few hours of the sediment drying if they cannot find an aquatic refuge (*e.g.* perennial section, hyporheic zone, lateral pond). Other aquatic taxa can tolerate a dry period of a few days if the streambed sediments remain relatively moist (Stanley *et al.*, 1994), while some aquatic taxa (*e.g.* some Chironomidae, Copepoda, Cladocera) can persist in dry sediments for several months as desiccation-resistant forms (Harper & Hynes, 1970; Williams & Hynes, 1976; Boulton, 1989; Tronstadt, Tronstadt & Benke, 2005). As a result, the duration of the dry period in temporary rivers may have a considerable influence on the aquatic invertebrate assemblage (*e.g.* overall density, diversity and structure) and its response to subsequent inundation (Larned *et al.*, 2007). Aquatic invertebrates persisting in streambed sediments during dry phases have been proposed to form an "invertebrate seedbank", which may facilitate recovery of the benthos after rewetting (Boulton, 1989; Tronstadt *et al.*, 2005; Larned *et al.*, 2007; Stubbington *et al.*, 2009). However, the contribution of invertebrate seedbanks to the persistence of the benthos in temporary rivers has not yet been quantified. During aquatic-terrestrial transition periods, invertebrate assemblages may also shift in composition as a consequence of the colonization of dry riverbeds by terrestrial invertebrates from adjacent fringing habitats (Wishart, 2000; Greenwood & McIntosh 2010; Corti *et al.*, 2011; Steward *et al.*, 2011). Although terrestrial successions in dry riverbeds have not yet been described, invertebrate assemblages from dry riverbeds and lateral riparian zones may converge over time.

We examined the effects on terrestrial and aquatic invertebrate assemblages of experimental rewetting of dry sediments collected from 13 sites located along a 15-km temporary reach of the Albarine River, France. Sites along the study reach had previously been dry for between 0.1 and 142 days. Dry sediments were collected from the dry streambed (DS) and from riparian gravel bars (RGB). We first predicted that invertebrate responses to rewetting would vary with the duration of the preceding dry period. Second, we predicted a convergence of invertebrate assemblage composition from rewetted DS and RGB sediments with increasing duration of the dry period. Third, if there is a significant contribution of the invertebrate seedbank to recovery upon rewetting, we predicted that invertebrate assemblages from rewetted DS sediments and benthic assemblages before and after dry periods would have many taxa in common.

METHODS

Study sites

The Albarine River drains a 313 km^2 catchment in temperate eastern France (**Figure 1**). For a 15 km stretch, the downstream section of the river flows across an alluvial plain underlain by thick (> 36 m) glacio-fluvial deposits, the permeability of which ranging from 2 10^{-2} to 7 10^{-2} m s^{-1} (Datry *et al.*, 2011). Along this alluvial plain, the river continuously infiltrates into the underlying aquifer, which gradually leads to complete river drying (**Figure 1**). Drying typically starts in spring at the confluence with the Ain River, and the drying front then progressively moves upstream throughout the summer. Flow generally resumes in late autumn/early winter (Larned *et al.*, 2011; Datry 2011; Datry *et al.*, 2011). In 2010, the onset of drying started in mid-May at the confluence (**Figure 1**), and the complete rewetting of the river occurred in late October.

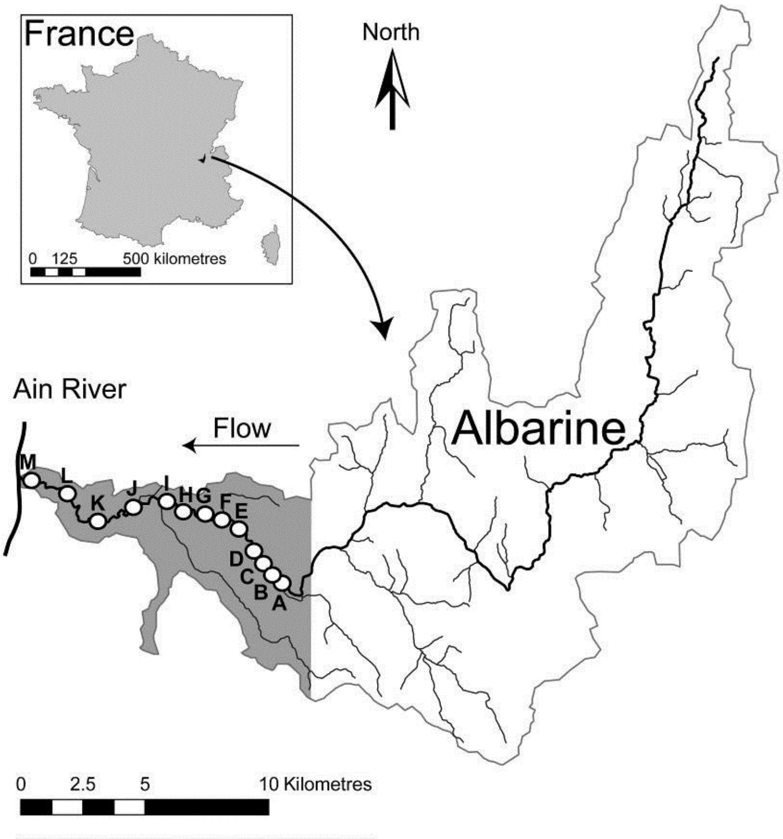


Figure 1 Map of the Albarine River catchment, France, showing perennial and temporary sections. Letters along the mainstem indicate sampling locations.

Thirteen sites with different dry periods were selected along the temporary section of the river (**Figure 1**). The dry period at each site was estimated at the time of sampling from the time elapsed since the last observed flow, on 14 May 2010. Between the onset of drying at site M and the 20 September, sites were visited every 1–10 days to allow an estimation of the dry period to the nearest 10 days. Sites G to M were sampled on 20 September 2010. The drying reach was then visited daily to estimate the dry period duration to within one hour. Sites A to F were sampled on 10 October 2010. As a result, site A was just drying (1.5 hour, 0.1 day), whereas site M had been dry for 142 days at the time of sampling; the remaining 11 sites were positioned along this gradient of dry period duration (**Table 1**).

Invertebrate responses to experimental rewetting

At each site, two or three dry sediment samples were collected from random points in riffles within the dry streambed (DS) (**Table 1**). Except at sites C, D, E and F, two dry sediment samples were also collected at the same time from random points from one adjacent dry riparian gravel bar (RGB) (**Table 1**). Gravel bars were located 2-4 m laterally from the river at mean flow conditions and had little vegetation at the time of sample collection. No differences in grain size were apparent between sediments from the riverbed and adjacent gravel bars. Each sample consisted of 2.5 L of sediment, which was manually excavated from a 0.2 m^2 surface area to a depth of about 10 cm and then placed in an 8 L container. In addition, two additional 1 L sediment samples were collected from the DS and RGB sampling areas, transferred to plastic bags and sealed for determination of sediment moisture. All samples were transported to the laboratory within 4 hr. Samples for the determination of sediment moisture content were immediately frozen and processed within 4 weeks. The 8 L containers were placed immediately in an environmental chamber (12h:12h light:dark cycle, 20 °C). Each container was flooded with 5 L of filtered, non-chlorinated tap water, continuously aerated using airstones, and fitted with 1-mm mesh lids to retain emerging insects. Immediately after water was added, and subsequently at t = 4, 8, 16 and 32 days, the water column of each container was swept vigorously using a 200 μm hand-net for 30 s to collect living aquatic and dead terrestrial invertebrates. Material retained on the mesh was preserved in 96 % ethanol. A wet period of 32 days was selected as a compromise between a long duration that could result in sediment anoxia, and one too brief for eggs and cysts to hatch (Larned *et al.*, 2007). After 32 days, the sediments in each container were vigorously elutriated six times and each elutriate poured through a 200 µm mesh sieve; retained material was preserved in 96 % ethanol.

Table 1. Sites, duration of the dry period and number of sediment samples collected for artificial rewetting and sediment moisture content. DS, dry streambed; RGB, riparian gravel bars.

Site	Dry period duration (days)	Sediment samples for rewetting		Sediment samples for % moisture	
		DS	RGB	DS	RGB
A	0.1	3	2	2	2
B	0.5	3	2	2	2
C	0.9	3	x	2	2
D	2	3	x	2	2
E	5	3	x	2	2
F	7	3	x	2	2
G	9	3	2	2	2
H	25	3	2	2	2
I	40	2	2	2	2
J	50	2	2	2	2
K	100	2	2	2	2
L	130	2	2	2	2
M	142	2	2	2	2
	total	34	18	26	26

Sediment moisture content

For each 1 L sediment sample, two subsamples of ~50 mL were weighed wet, dried at 60 °C to constant mass and reweighed. Moisture content was determined from differences in wet and dry mass.

The benthos

At five sites (E, F, H, K and M), samples of benthic invertebrates were collected before and after drying events, for comparison with invertebrate assemblages from experimentally rewetted sediments. Benthic samples before drying were collected in early May 2010, 13 days before the section started to dry, and post-drying benthic samples were collected in November 2010, 21 days after the entire section rewetted. At each site, four benthic samples were collected at random from two riffles. Invertebrates were sampled using a Hess sampler (200 µm mesh, 0.125 m^2 in diameter, down to a 10 cm depth) and were preserved in 96 % ethanol.

Invertebrates were identified to the lowest taxonomic level possible, which varied with taxonomic group and developmental stage. Most aquatic insects and mollusks were determined to the genus level, Chironomidae and most terrestrial insects were identified at the family level and other taxa at the family, order or class level. Taxa were classified as aquatic, semi-aquatic, aerial stages of aquatic taxa, or terrestrial (Tachet *et al.*, 2000). Semi-aquatic taxa included those for which a definite assignment to aquatic or terrestrial classes could not be made, mainly because of the low taxonomic resolution (*e.g.* Acarina, Oligochaeta, Nematoda).

Data analysis

Faunal differences between dry streambed and riparian gravel bar sediments

Invertebrates recovered from the water column and from the sediments during and at the end of the rewetting experiment were pooled together. Non-parametric Wilcoxon sum-rank tests were used to compare taxonomic richness and total density for all invertebrate classes (i.e. aquatic, semi-aquatic, aerial stages of aquatic taxa and terrestrial), and sediment moisture content between DS and RGB sediments.

Effects of the length of the dry period on invertebrate assemblages

Linear and non-linear regressions were used to examine relationships between the duration of the preceding dry period and taxonomic richness and density for all invertebrate classes and sediment moisture content of DS and RGB sediments. Compositional changes in DS and RGB invertebrate assemblages with an increasing dry period were examined using non-metric multidimensional scaling (NMDS). Similarity matrices were calculated using Bray-Curtis distances on log-transformed density data. Both for DS and RGB, nestedness analysis was used to examine if the invertebrate taxa (all classes considered) collected at sites with a long preceding dry period duration were nested subsets of taxa found at sites with a shorter preceding dry period. A detailed explanation of nestedness analysis is given in Atmar & Patterson (1993). Briefly, nestedness analyses operate on matrices of sites versus taxon presence and absence data. A nestedness calculator reorders the rows and columns of the matrix until the cells with taxa present are concentrated into one corner of the matrix (i.e. the matrix is "packed" with as few empty cells as possible). An index of nestedness (T, temperature) is then calculated from a comparison of the observed (packed) matrix with a maximally nested matrix. Monte-Carlo permutation tests are used to generate random matrices, and the probability that the observed nestedness has occurred by chance is determined by comparing the observed T with T-values from the random matrices. Bray-Curtis similarity between DS and RGB sediments were calculated on log-transformed density data from the 9 sites (A, B, G, H, I, J, K, L and M) where both sample types were collected, and examined along the gradient of increasing dry period duration.

Experimentally rewetted sediment and benthic invertebrates

The occurrence of each taxon among the different sample types (pre- and post-drying benthic invertebrate samples and rewetted DS sediment samples) was examined for the five sites (E, F, H, K and M) at which all sample types were collected. Bray-Curtis similarities were then calculated to examine assemblage similarities among the three sample types. Invertebrate assemblages could not be compared quantitatively, as sampling techniques differed, so similarities were calculated based on presence-absence data. This analysis was conducted for all taxa occurring simultaneously in the three datasets and then terrestrial taxa removed to focus on aquatic and semi-aquatic taxa.

All statistical analyses were performed using R software (R Development Core Team, 2011). The significance level for all statistical analyses was set at $P = 0.01$.

RESULTS

Fauna of the dry streambed and riparian gravel bar sediments

A total of 21 539 individuals belonging to 73 taxa were recovered from experimentally rewetted sediments (**Appendix S1**). From DS sediments, 18 470 individuals (72 taxa) were collected, of which 86 % were aquatic (46 taxa), 8 % semi-aquatic (seven taxa), 6 % aerial stages of aquatic taxa (four taxa) and <1 % terrestrial individuals (18 taxa). From RGB sediments, 2 747 individuals (52 taxa) were collected, of which 33 % were aquatic (28 taxa), 56 % semi-aquatic (seven taxa), 1 % aerial stages of aquatic taxa (seven taxa) and 10 % terrestrial individuals (15 taxa). The two most abundant aquatic taxa were Cladocera (59.1 %) and Cyclopoida (9.2 %) for DS, and Cladocera (13.2 %) and Ostracoda (11.6 %) for RGB sediments. Oligochaeta was the most abundant semi-aquatic taxon in both DS (6.7 %) and RGB (33.5 %) sediments. Adult Chironomidae were the most abundant aerial stages of aquatic taxa in DS (4.3 %) and RGB (1.6 %) sediments. Hemiptera was the most abundant terrestrial taxon in DS sediments (0.2 %), whereas Thysanoptera (0.6 %) was the most abundant terrestrial taxon in RGB sediments.

There were no differences between DS and RGB sediments in the taxonomic richness of total, aquatic, semi-aquatic or aerial stages of aquatic taxa. In contrast, the number of terrestrial taxa was higher in RGB than in DS sediments (**Table 2**, Wilcoxon sum-rank test, $P = 0.006$). The overall densities of total and aquatic taxa were higher on DS than on RGB sediments (**Table 2**, Wilcoxon sum-rank test, $P = 0.003$). The density of aerial stages of aquatic taxa did not differ between sample types. Semi-aquatic and terrestrial densities were higher in RGB than on DS sediments (**Table 2**, Wilcoxon sum-rank test, $P = 0.008$ and *0.001*, respectively). Sediment moisture content was higher in RGB than in DS sediments (10.5 ± 4 % and 6.5 ± 2 %, respectively, Wilcoxon sum-rank test, $P = 0.002$).

Duration of the dry period

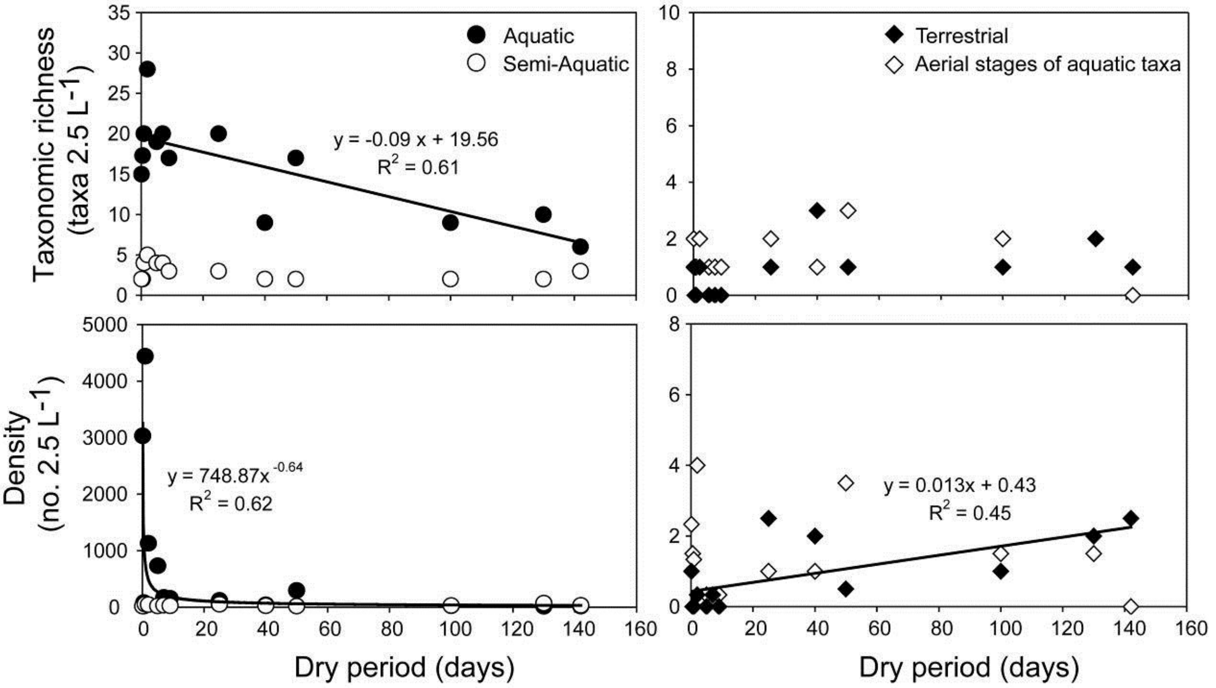
Dry streambed sediments

Aquatic taxon richness decreased steadily along the gradient of increasing dry period duration (**Figure 2a**). On average, for every 10-day increase in the dry period, ~1 aquatic taxon was lost from DS sediments. Semi-aquatic, aerial stages of aquatic taxa and terrestrial taxon richness did not show any relationship with length of the dry (**Figure 2a**). In contrast, the density of aquatic taxa declined as a power function of increasing duration of the dry period (**Figure 2a**). An increase in the dry period duration from 0.1 to 10 days resulted in a 20-fold decrease in the density of aquatic invertebrates. For preceding dry period from 7 to 142 days, there was no substantial change in the density of aquatic taxa, which remained below 50 organisms $2.5L^{-1}$. Terrestrial density increased steadily with length of the dry period (**Figure 2a**). However, after 142 days of drying, mean terrestrial density on DS sediments was only 2 ± 1 organisms $2.5L^{-1}$. Density of semi-aquatic taxa and aerial stages of aquatic taxa did not change with increasing dry period duration.

Table 2. Minimum, maximum, and mean (± S.D.) of total, aquatic, semi-aquatic, aerial stages of aquatic taxa and terrestrial richness and density recovered in rewetted sediments from the dry streambed (DS) and riparian gravel bars (RGB). Values are given for 2.5 L of sediments.

	DS				**RGB**			
	Min.	**Max.**	**Mean**	**± SD**	**Min.**	**Max.**	**Mean**	**± SD**
Total Richness	15	39	23.9	± 7.4	12	27	19.4	± 4.7
Aquatic Richness	6	28	15.3	± 6.3	5	19	9.9	± 4.9
Semi-aquatic Richness	2	5	2.9	± 1.0	2	5	3.1	± 0.9
Aerial Richness	0	3	1.5	± 0.8	0	2	1.0	± 0.7
Terrestrial Richness	0	3	1.2	± 1.2	1	8	3.8	± 2.7
Total Density	44	4532	980.7	± 1382,3	29	482	214.4	± 140.2
Aquatic Density	15	4439	918.2	± 1382.1	11	424	113.5	± 128.7
Semi-aquatic Density	20	72	35.1	± 16.2	29	147	70.4	± 37.7
Aerial Density	0	4	1.4	± 1.2	0	4	1.1	± 1.2
Terrestrial Density	0	2.5	1	± 1	2	148	21.9	± 47.2

a) DS sediments



b) RGB sediments

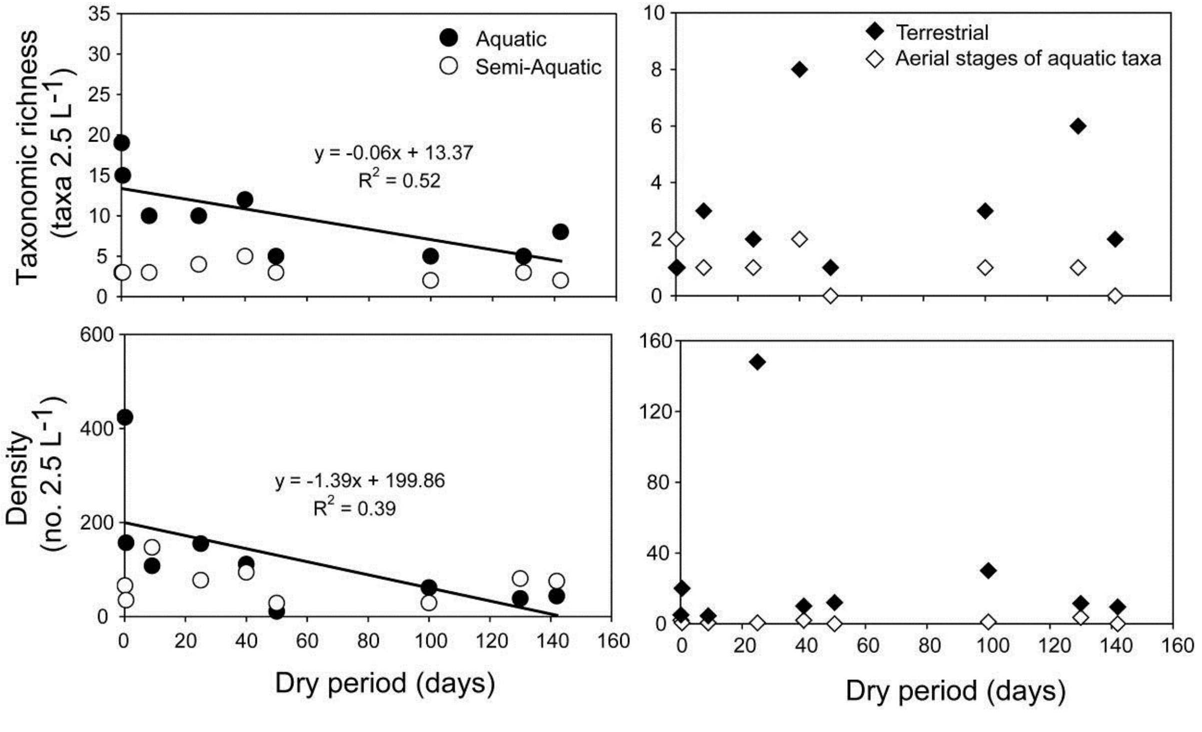
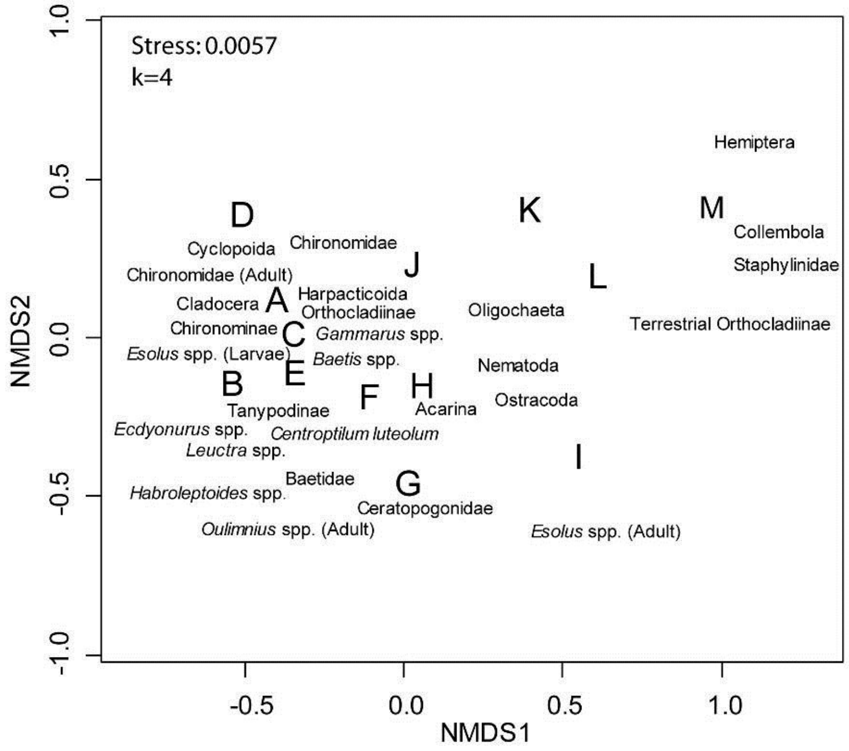


Figure 2 Relationships between duration of the dry period and taxonomic richness and density of aquatic, semi-aquatic, aerial stages of aquatic taxa, and terrestrial taxa from (a) dry streambed (DS) and (b) riparian gravel bar (RGB) sediments.

The NMDS plot showed a clear separation of sites according to the duration of dry period, from A on the left-hand side to M on the right-hand side (**Figure 3a**). The density of aquatic taxa, such as Cyclopoida, Harpacticoida, Cladocera and Diptera larvae (e.g. Chironomidae Orthocladiinae and Tanypodinae), Ephemeroptera (e.g. Baetis spp.) and Coleoptera (e.g. Esolus spp.), were high sites with a preceding dry period < 1 week (A, B, C, D and E) (**Figure 3a**). Sediments from sites with a preceding dry period between 7 to 40 days (F, G, H) high a density of aquatic taxa, such as larvae of Diptera (e.g. Ceratopogonidae), Ephemeroptera (e.g. Baetidae, *Centroptilum* luteolum; Müller, 1776, Habroleptoides spp.), Coleoptera (e.g. Oulimnius spp.) and Plecoptera (Leuctra spp.) and semi-aquatic taxa such as Acarina (**Figure 3a**). Sediments from sites with a long preceding dry period (> 40 days, I, J, K, L, M) had a high density of aquatic taxa, such as Ostracoda or Coleoptera (adult Esolus spp.), a high density of semi-aquatic taxa such as Collembola, Nematoda, Oligochaeta, and a high density of terrestrial taxa such as Orthocladiinae larvae, Staphylinidae, and Hemiptera (**Figure 3a**).

Nestedness analyses indicated that DS sediment invertebrate assemblages were not random, but nested along the gradient of increasing duration of the dry period ($T = 23.1$, Monte-Carlo permutation test, $P < 0.001$). This indicated that invertebrate assemblages found at the most depauperate sites, those with the longest preceding dry period, were subsets of assemblages found at richest sites, which were those that had dried most recently.

a) DS sediments



b) RGB sediments

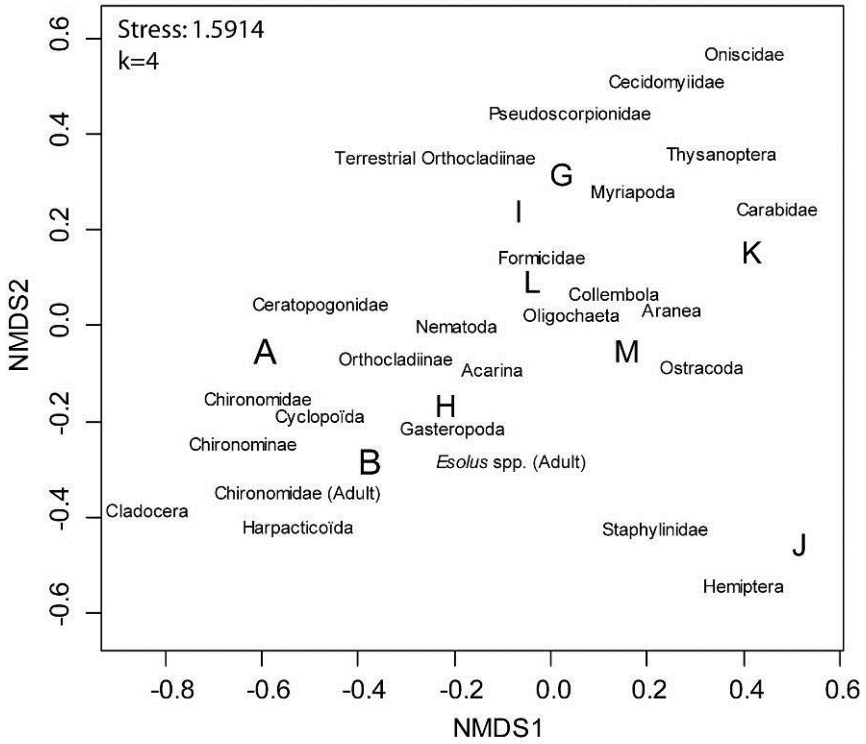


Figure 3 Two-dimensional NMDS plots, based on log-transformed density data, of invertebrate assemblages recovered from rewetted sediments collected from (a) dry streambeds (DS) and (b) riparian gravel bars (RGB).

Riparian gravel bar sediments

Aquatic taxon richness decreased steadily along the gradient of increasing duration of the dry period (**Figure 2b**). On average, for every 20-day increase in duration of the dry period, ~1 aquatic taxa was lost from the sediments. Semi-aquatic, aerial stages of aquatic taxa and terrestrial taxon richness did not show any relationship with duration of the dry (**Figure 2b**). The overall density of aquatic taxa decreased steadily with increasing duration of the dry period, with an average ~12 individuals being lost from invertebrate assemblages for every 10-day increase in the duration of the dry period (**Figure 2b**). Overall densities of semi-aquatic taxa, aerial stages of aquatic taxa and terrestrial taxa did not change with increasing duration of the dry period.

The NMDS ordination showed a poor separation of sites according to duration of the dry period (**Figure 3b**). However, RGB sediments from sites with a preceding dry period < 1 day (A and B) and site H (with a dry period duration of 25 days) were grouped together, and had high densities of aquatic taxa, such as Cyclopoida, Harpacticoida, Cladocera or Diptera larvae (*e.g.* Ceratopogonidae, Chironomidae, Chironominae and Orthocladiinae) (**Figure 3b**). RGB sediments from other sites, with a preceding dry period duration > 9 days, were on the right-hand side of the NMDS ordination and had high densities of terrestrial taxa, such as Oniscidae, Myriapoda, Pseudoscorpionidae, Aranea, Formicidae, Cecidomyiidae, Carabidae and Thysanoptera and high densities of semi-aquatic taxa such as Oligochaeta, Acarina, Nematoda and Collembola (**Figure 3b**). Sediments from site J were isolated from the others sites, because of higher densities of terrestrial Staphilinidae and Hemiptera (**Figure 3b**).

RGB sediment invertebrate assemblages were randomly distributed along the gradient of duration of the dry period and showed no nestedness (T = 44.6, Monte-Carlo permutation test, $P = 0.65$).

Sediment moisture content

Sediment moisture content of DS sediments decreased very rapidly with increasing duration of the dry period (**Figure 4**). Within the first 20 days of drying, sediment moisture content was more than halved, from 15 to 7 %. In contrast, RGB sediment moisture content showed no relationship with increasing duration of the dry period (**Figure 4**).

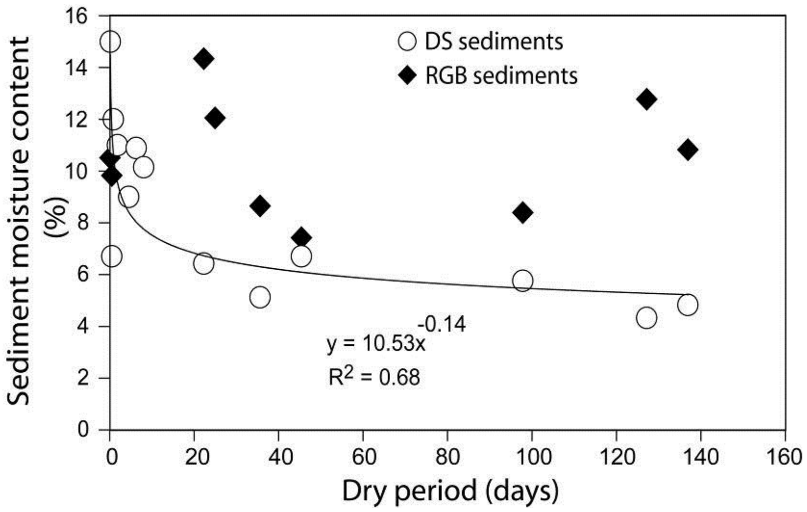


Figure 4 Relationships between duration of the dry period and sediment moisture content for DS (Open circle) and RGB (closed diamond) sediments. The regression line fits duration of the dry period to DS sediment moisture content.

Convergence of DS and RGB invertebrate assemblages with increasing duration of the dry period

Similarity between DS and RGB invertebrate assemblages decreased steadily from 60 to 40 % as the duration of the dry period increased from 0.1 to 40 days (**Figure 5**). Between 40 and 50 days after drying, similarity between DS and RGB samples was halved. After 50 dry days, similarity between sample types increased steadily to reach 60 % after 130 days of drying.

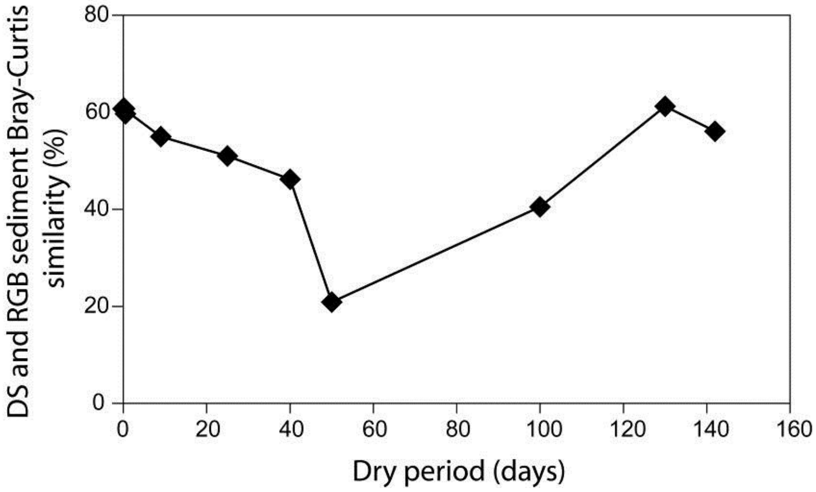


Figure 5 Relationships between duration of the dry period and log-transformed density Bray-Curtis similarity between DS and RGB sediments.

Experimentally rewetted sediment and benthic invertebrates

A total of 33 taxa were found in pre-drying benthic samples, 31 in DS sediments and 47 in post-drying benthic samples (**Appendix S1**). Thirty-one taxa were common to pre- and post-drying benthic invertebrate assemblages, of which 20 taxa were also found in experimentally rewetted DS sediments. The taxa common to all sample types comprised Ephemeroptera (*Baetis* spp., *Ecdyonurus* spp., *Habroleptoides* spp., *Centroptilum luteolum*), Plecoptera (*Leuctra* spp.), Trichoptera (*Hydropsyche* spp.), Coleoptera (*Esolus* spp. and *Limnius* spp.), Diptera (Ceratopogonidae, Chironomidae, Chironominae, Psychodidae, Orthocladiinae, Tanypodinae), *Gammarus* spp. (Amphipoda), Cyclopoida, Harpacticoida, Ostracoda, Oligochaeta and Nematoda. Therefore, the number of aquatic taxa recovered from the experimentally rewetted DS sediments represented on average 65 % of the taxa present in pre- and post-drying benthic. This proportion did not change substantially with an increasing dry period and ranged from 53 to 69 % at the five sites considered, despite the fact that post-drying taxonomic richness and density of the benthos decreased as the preceding dry period increased (R^2 = 0.49 and 0.74, respectively). In terms of density, the number of individuals of each of the 20 aquatic taxa recovered from rewettedsediment samples, and common to all sample types, ranged from 1 to 38 individuals, with an average of 7 organisms $2.5L^{-1}$ of sediment.

Similarity analysis showed that pre and post-drying benthic invertebrate samples were relatively similar in composition, with 60 $\pm$ 4 % (mean $\pm$ S.D.) similarity (**Figure 6**). Pre-drying benthic samples and DS sediments were 29 $\pm$ 10 % similar, whilst DS sediments and post-drying benthic samples were 24 $\pm$ 9 % similar (**Figure 6**). These similarities between DS sediments and both pre- and post-drying samples did not change with increasing duration of dry period. In addition, when considering only aquatic and semi-aquatic taxa, these similarities increased only slightly (**Figure 6**).

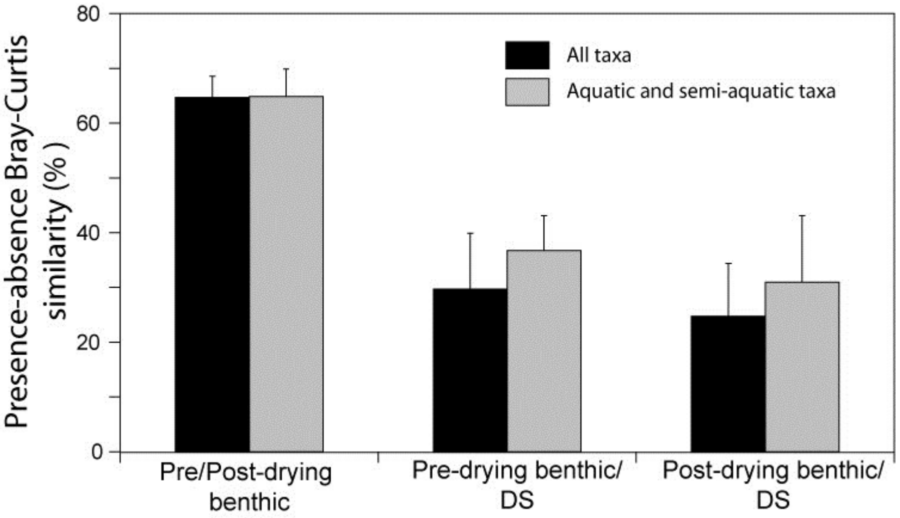


Figure 6 Presence-absence Bray-Curtis similarities between pre- and post-drying benthic invertebrate assemblages and DS invertebrate assemblages.

DISCUSSION

Duration of the dry period

Until recently, dry sediments in temporary rivers were considered as "biologically inactive" (Stanley, Fischer & Grimm, 1997), but several studies have refuted this assumption. In particular, some aquatic invertebrates can persist for several weeks or months in dry sediments and then recolonize benthic habitats after flow resumes (Brock *et al.*, 2003; Tronstadt *et al.*, 2005; Larned *et al.*, 2007; Stubbington *et al.*, 2009). Moreover, some terrestrial invertebrates from adjacent riparian zones colonize riverbeds and contribute to the biological activity of dry sections (Greenwood & McIntosh, 2010; Corti *et al.*, 2011). In our study, we simulated the onset of flow by artificially rewetting dry sediments which had previously been exposed to a wide range of dry period durations. Our first prediction, that invertebrate responses to rewetting would vary with duration of the preceding dry period, was largely supported by the results. Artificial flooding of dry sediments led, within 32 days, to the appearance of aquatic invertebrate taxa in all samples. Since there was no possibility of aerial colonization or drift, these aquatic invertebrates must have persisted as active or dormant (desiccation-resistant) life stages. In addition, terrestrial invertebrates were recovered from both rewetted DS and RGB sediments.

The taxon richness of aquatic organisms decreased linearly with increasing duration of the dry period in both DS and RGB sediments. In contrast, aquatic invertebrate density decreased as a power function of increasing dry period duration in DS sediments. This concurrent rapid decrease in density and linear decrease in richness suggests that many individuals from a small number of desiccation-sensitive taxa disappear soon after the temporary reach dries. However, a low diversity assemblage of resistant taxa persists during prolonged dry periods, as reported by Larned *et al.* (2007) and Stubbington *et al.* (2009) in temporary rivers in New Zealand and the United Kingdom, respectively. Desiccation-sensitive taxa in the Albarine River included several Ephemeroptera (*Baetis* spp., *Centroptilum luteolum*, *Habroleptoides* spp.), Plecoptera (*Leuctra* spp.), and Coleoptera (*Esolus* spp., *Oulimnius* spp.). These taxa were present exclusively in sediments that had experienced very short (< 7 days) dry periods, and thus remained relatively moist. These taxa may have some capacity for avoiding desiccation for short periods, such as crawling to moist benthic or hyporheic sediments. At the opposite end of the spectrum, desiccation-resistant taxa were those found in sediments after long (> 4 weeks) dry periods and included the Cyclopoida, Ostracoda and Nematoda. Desiccation-resistant stages are well-known in Cyclopoida and Ostracoda (*e.g.* Dahms, 1995; Dole-Olivier *et al.*, 2000), and the presence of copepodites in rewetted samples after long dry periods indicated hatching from desiccation-resistant eggs. Possible density-dependent emergence or mortality may occur during the initial phases of streambed drying, as indicated by the relationships between aquatic density and taxonomic richness with duration of the dry period (Larned *et al.*, 2007). However, these processes are still poorly studied and require more experimental research.

These relationships with duration of the dry period have practical consequences for management of temporary rivers. Indeed, artificial increases in the duration of the dry period, for example due to groundwater abstraction, surface water diversion or climate change, will inevitably reduce the richness and density of benthic invertebrate assemblages when flow resumes. In this study, each 10-day increase in the dry period removed approximately one taxon from the assemblage. This rate is much higher than that reported from a New Zealand temporary river (Selwyn River, with one taxon removed every 50 days increase in the dry period, Larned *et al.*, 2007). However, the Albarine River seedbank was also much richer in taxa that that in the Selwyn River.

Two types of "terrestrial" invertebrates were recovered from rewetted sediments: flying adults with aquatic larvae and riparian terrestrial taxa. Flying adults (Baetidae, Leuctridae and Chironomidae) were found exclusively in DS sediments and mostly after 8 d of rewetting, indicating they were not collected in the field as adults, but as larvae. Although they showed no relationships with the length of the dry period, most were collected in sediments with dry period < 50 days. Flying Ephemeroptera and Plecoptera clearly originated from the emergence of desiccation-sensitive Baetidae and Leuctridae, present in the sediments shortly after drying, and their late (October) emergence could an adaptation of the life cycle to summer drying events. In contrast, adult Chironomidae were collected in sediments with longer dry periods (40 to 142 days) and may have originated from emergence of some desiccation-resistant larvae (Tronstadt *et al.*, 2005). The density of terrestrial invertebrates (Coleoptera, Orthocladiinae, Hemiptera) increased with the duration of dry period in DS but not in RGB sediments, suggesting a progressive colonisation of the dry streambed (Corti *et al.*, 2011; Steward *et al.*, 2011). After a prolonged (142 days) dry period, however, the density of terrestrial taxa in DS sediments was still 20-fold lower than in adjacent RGB sediments. In addition, terrestrial invertebrates from RGB sediments showed little changes in composition with increasing duration of the dry period, suggesting that the presence or absence of aquatic prey in DS sediments was not an important driver of RGB terrestrial assemblages. Riparian predators may be able to modify their diet according to the prey types (aquatic or terrestrial) available. However, this requires confirmation using stable isotopes (Paetzold *et al.*, 2005), for example, or gut content analysis (Hering & Plachter, 1997).

Convergence of DS and RGB invertebrate assemblages during dry phases

Invertebrate composition in DS and RGB sediments did not increase in similarity during dry phases. After 142 days of drying, DS sediments still harboured much lower density and richness of terrestrial organisms, and several riparian taxa found on RGB (*e.g.* Carabidae, Aranea, Oniscidae) were not recovered from DS sediments. Habitat characteristics may differ considerably between DS and RGB sediments; for instance, DS sediment moisture content was much lower than RGB sediments. This could be due to differences in streambed shading, sediment composition (Allen, 1970) or gravel bar vegetation (Brosofske *et al.*, 1997; Chen *et al.*, 1999). However, these parameters are typically not measured and this notion is speculative. In addition, DS assemblages were typically nested along the gradient of increasing duration of the dry period, indicating that invertebrate assemblages from sites experiencing the longest dry periods were subsets of assemblages from sites with shorter dry period durations. Such nestedness along the drying gradient has been reported previously (Arscott *et al.*, 2010; Datry, 2011) and seems to be common in temporary rivers, as drying often follows a longitudinal pattern (Larned *et al.*, 2011). However, no nestedness was detected in invertebrate assemblages from RGB sediments. These results suggest that temporal and spatial transition zones in temporary rivers have distinct biodiversity dynamics. The presence of spatial and temporal ecotones in river corridors increases habitat heterogeneity, which can increase biodiversity at the landscape scale (Ward & Tockner, 2001). In addition, longitudinal gradients of dry and wet periods in temporary rivers like the Albarine River increase successional diversity (i.e. there are mosaics of dry and saturated riverbed patches at various stages of terrestrial and aquatic succession) (Ward, Malard & Tockner, 2002; Larned *et al.*, 2007).

Experimentally rewetted sediment and benthic invertebrates

According to Lake (2003), resilience is a measure of the rate of recovery of a community following a disturbance. The survival of aquatic invertebrates in dry river sediments following the loss of surface water has been reported from temporary rivers located in different climatic zones (Boulton, 1989; Tronsdtad *et al.*, 2005; Larned *et al.*, 2007; Stubbington *et al.*, 2009). However, the contribution of this mechanism to the recovery of benthic invertebrates was never quantified. In the Albarine River, more than half of the aquatic taxa found in the benthic zone both before and after summer drying events were also recovered from rewetted sediments, suggesting that the invertebrate seedbank could contribute substantially to the benthic invertebrate assemblage resilience. Nevertheless, assemblages in before/after benthic samples and DS sediments were rather different, suggesting that recovery dynamics after rewetting were probably taxon-specific and that other colonisation mechanisms have occurred. Although benthic invertebrate richness and density decrease with increasing duration of the dry period in the Albarine River (Datry, 2011), as in other temporary rivers (*e.g.* Datry, Larned & Scarsbrook, 2007; Arscott *et al.*, 2010), the proportion of common taxa found in DS sediments and in before/after benthic samples remained interestingly constant in the Albarine River across sites with different dry period duration. Therefore, the persistence of aquatic taxa in streambed sediments during dry phases could be an important means of maintaining aquatic invertebrate biodiversity in temporary rivers, particularly when streambed sediments remain sufficiently moist during dry periods. This conclusion highlights the importance of protecting dry reaches in temporary rivers, which are often impaired by recreation, sediment mining or sewage pollution (Larned *et al.*, 2010).

Additional processes must occur following flow resumption to explain the rapid recolonisation of rewetted benthic sediments by aquatic invertebrates. Ten taxa, representing 35 % of benthic assemblage taxa, were not found in rewetted samples. Deeper hyporheic sediments are probably a poor refugium in the Albarine River during long dry periods, because they dry up completely after 5 to 15 days (Datry, 2011). Therefore, drift, aerial migration and oviposition require quantification following flow resumption, to improve our understanding of the recolonisation dynamics of rewetted benthic habitats in temporary rivers (Williams & Hynes, 1976; Boulton, 1989; Stanley *et al.*, 1994).

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Appendix S1. **List of the taxa with their classification as aquatic (A), semi-aquatic (S), aerial stage of aquatic taxa (AS) and terrestrial (T) recovered from rewetted sediment samples (dry streambed and riparian gravel bars) and pre- and post-drying benthic samples.**

	Classification	**Rewetted sediment samples**	**Pre-drying benthic samples**	**Post-drying benthic samples**
Insects				
Coleoptera				
Carabidae	T	1		
Chrysomelidae adult	T	1		
Coelostoma spp.	A		1	
Dryops spp.	A	1		
Elmis spp.	A		1	1
Esolus spp.	A	1	1	1
Helichus spp.	T	1		
Hydraena spp.	A		1	1
Limnius spp.	A	1	1	1
Oulimnius spp.	A	1		1
Staphylinidae	T	1		
Diptera				
Athericidae	A		1	1
Cecidomyiidae nymphs	T	1		
Cecidomyiidae	T	1		
Ceratopogonidae	A	1	1	1
Ceratopogoninae	A	1		1
Chironomidae adult	AS	1		
Chironomidae nymph	AS	1		
Chironomidae	A	1	1	1
Chironominae	A	1	1	1
Empididae	A	1		1
Leptoconopinae	A	1		
Limoniidae	A		1	1
Orthocladiinae	A	1	1	1
Orthocladiinae	T	1		
Psychodidae	S	1	1	1
Rhagionidae	A	1		
Simuliidae	A		1	1
Stratiomyidae	S	1		
Tabanidae	A	1		
Tanypodinae	A	1	1	1
Tipulidae	S	1		
Ephemera				
Baetidae adult	AS	1		
Baetidae nymph	AS	1		
Baetis spp.	A	1	1	1
Caenis spp.	A		1	
Centroptilum luteolum (Müller, 1776)	A	1	1	1
Ecdyonurus spp.	A	1	1	1
Ephemera spp.	A		1	1
Ephemerella spp.	A		1	
Habroleptoides spp.	A	1	1	1
Leptophlebiidae nymph	AS	1		
Rhithrogena spp.	A		1	1
Torleya major (Klapálek, 1905)	A			1
Hemiptera				
Aphidoidea	T	1		
Undetermined	T	1		
Heteroptera				
Undetermined	T	1		
Hymenoptera				
Formicidae	T	1		

Undetermined	T	1		
Lepidoptera				
Psychidae	T	1		
Mallophaga				
Undetermined	T	1		
Plecoptera				
Chloroperla spp.	A		1	
Leuctridae adult	AS	1		
Leuctridae nymph	AS	1		
Leuctra spp.	A	1	1	1
Nemoura spp.	A			1
Psocoptera				
Undetermined	T	1		
Thysanoptera				
Undetermined	T	1		
Trichoptera				
Glyphotaelius pellucidus (Retzius, 1783)	A	1		1
Hydropsyche spp.	A	1	1	1
Hydroptila spp.	A			1
Lepidostoma spp.	A			1
Mystacides spp.	A	1	1	
Limnephilinae	A			1
Odontocerum albicorne (Scopoli, 1763)	A	1		1
Polycentropus spp.	A	1		1
Psychomyia pusilla (Fabricius, 1781)	A			1
Rhyacophila spp.	A		1	1
Sericostoma spp.	A		1	1
Crustaceans				
Cladocera	A	1		
Cyclopoida	A	1	1	1
Harpacticoida	A	1	1	1
Ostracoda	A	1	1	1
Amphipoda				
Gammarus spp.	A	1	1	1
Niphargus spp.	A	1		1
Isopoda				
Asellus spp.	A	1		1
Oniscidae	T	1		
Arachnids				
Aranea	T	1		
Acarina	S		1	1
Pseudoscorpionidae	T	1		
Myriapods	T	1		
Collembola	S	1		
Annelids				
Acheta	A			
Erpobdella spp.	A		1	1
Oligochaeta	S	1	1	1
Nemahelminths	S	1	1	1
Plathyhelminths				
Dendrocoelidae	A			1
Dugesiidae	A	1		1
Planariidae	A			1
Cnidaria				
Hydra spp.	A	1		1
Molluscs				
Limnaeidae	A		1	
Radix spp.	A	1		
Sphaeridae	A	1		
Sphaerium spp.	A			1
Valvata cristata (Müller, 1774)	A	1		1
Eggs		1		

ANNEXE 3

LISTE DES PUBLICATIONS ET COMMUNICATIONS

Articles publiés (ou soumis)

Corti R., Larned S.T., and Datry T., in revision. A comparison of pitfall-trap and quadrat method for sampling ground-dwelling invertebrates in dry riverbeds. *Hydrobiologia*

Corti R. and Datry T., 2012. Invertebrates and sestonic matter in an advancing wetted front travelling down over a dry riverbed (Albarine, France). *Freshwater Science*. 31,1187-1201

Courtin O. et Corti R., 2012. Agyrtes (agyrtecanus) bicolor (Laporte de Castelnau, 1840) : une espèce bien implantée à l'Est de Lyon (Coleoptera, Staphylinoidea, Agyrtidae). *L'Entomologiste*. 68, 163-165

Datry T., Corti R., and Philippe M., 2012. Spatial and temporal aquatic-terrestrial transitions in the temporary Albarine River, France: responses of invertebrates to experimental rewetting. *Freshwater Biology*. 57, 716-727

Corti R., Datry T., Drummond L. and Larned S.T, 2011. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. *Aquatic Sciences*. 73, 537-550

Datry T., Corti R., Claret C., Philippe M., 2011. Flow intermittence controls leaf litter decomposition in a French river: the memory of drying. *Aquatic Sciences*. 73, 471-483

Participations à des congrès scientifiques

Corti R. and Datry T. "Colonization of dry river beds by terrestrial invertebrates". Juin 2012. *Louisville – Kentucky. Society for Freshwater Science Annual meeting 2012*.

Corti R., Charansol S. and Datry T. “Surfing the wave: invertebrate fluxes in the advancing wetted front of a temporary river following a 6 month dry period”. 01/07/2011. *Girona – Espagne. SEFS7.*

Corti R., Datry T., Drummond L. and Larned S. “Natural variation in immersion and emersion affects breakdown and invertebrate colonisation of leaf litter in a temporary river”. 26/01/2011. *Lyon – France. InBioProcess.*

Corti R., Datry T., Claret C. and Philippe M. “Flow intermittence controls leaf litter decomposition in a French temporary river: the importance of past drying events”. 11/06/2010. *Santa-Fe – Nouveau Mexique. ASLO & NABS summer meeting.*

Corti R., Datry T., Claret C. and Philippe M. “Leaf litter decomposition along a flow permanence gradient in a French temporary river”. 18/08/2009. *Sinaia – Roumanie. SEFS6.*

Roland **CORTI**

Assèchement des cours d'eau : effets sur les communautés d'invertébrés et la dynamique de la matière organique particulaire RESUME

Les transitions terrestre-aquatique jouent un rôle primordial dans le fonctionnement des écosystèmes. Dans les cours d'eau qui cessent de s'écouler périodiquement, ces transitions se développent latéralement au travers des zones ripariennes mais aussi longitudinalement le long du lit du cours d'eau. L'objectif de ce travail de thèse était de déterminer les effets de ces transitions terrestre-aquatique dans les lits des cours d'eau sur les communautés d'invertébrés terrestres et sur dynamique de la matière organique particulaire, un processus écologique fondamental au fonctionnement des cours d'eau. Les résultats montrent que communautés d'invertébrés ripariens sont peu dépendantes des ressources aquatiques du cours d'eau mais sont essentielles au maintien de la diversité en invertébrés dans les lits asséchés. La matière organique est transportée et se décompose par à coup lors des conditions aquatiques, influençant potentiellement la disponibilité en nutriments dans les réseaux hydrographiques.

Mots-clés : cours d'eau temporaires, écotones, transitions terrestre-aquatique, mosaïque d'habitats, méta-communautés, processus biogéochimique

When the rivers run dry: effects on invertebrate communities and particulate organic matter dynamic ABSTRACT

Aquatic-terrestrial transitions play a major role in the functioning of ecosystems. In rivers that periodically cease to flow, these transitions move laterally in riparian zones and longitudinally along dry riverbeds. The objective of this thesis was to determine in drying rivers the effects of aquatic-terrestrial transitions on terrestrial invertebrate communities and on particulate organic matter dynamic, a key ecological process for ecosystem functioning. The results show that riparian communities are poorly dependent on aquatic resources from the rivers but are essential to invertebrate diversity in dry riverbeds. Organic matter has a pulsed dynamic in drying rivers with transport and processing stages limited to aquatic conditions, potentially influencing nutrient availability in river networks.

Keywords : temporary rivers, ecotones, terrestrial-aquatic transitions, habitat mosaic, metacommunity, biogeochemical processes

DISCIPLINE

Ecologie

INTITULE ET ADRESSE DE L'U.F.R. OU DU LABORATOIRE

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