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Olivier DÉZERALD

Impacts des changements environnementaux sur la biodiversité néotropicale: réponses structurelles et fonctionnelles des réseaux trophiques faunistiques des broméliacées à réservoirs

Sous la direction de Céline LEROY et Régis CÉRÉGHINO

Soutenance prévue le 12 Novembre 2015 à l'UMR EcoFoG, Kourou

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tous ceux qui la liront . . .
en entier :)

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RESUMÉ

Les forêts néotropicales accueillent une importante biodiversité encore méconnue. L'intégrité des écosystèmes naturels est menacée par les changements environnementaux (*e.g.,* réchauffement climatique, destruction des habitats), par conséquent, identifier les facteurs structurants, naturels et anthropiques, du fonctionnement des écosystèmes, représente un défi scientifique crucial. L'inhérente complexité de ces milieux diversifiés pose de nombreux problèmes conceptuels et logistiques comme un échantillonnage exhaustif et/ou l'identification des espèces. Les broméliacées à réservoirs sont des écosystèmes miniatures adéquats pour pallier ces difficultés, car elles retiennent de l'eau de pluie et accumulent de la matière organique au creux de leurs feuilles, permettant ainsi de supporter des réseaux trophiques simples d'invertébrés aquatiques. Elles peuvent être échantillonnées exhaustivement, ont une forte abondance locale, et une large aire de répartition.

De l'échelle locale à biogéographique, les travaux de cette thèse visent d'abord à comprendre comment ces communautés se structurent en réponse à l'hétérogénéité naturelle des forêts amazoniennes (*e.g.,* ouverture de la canopée, fluctuations climatiques saisonnières), puis tente de prédire, par le biais d'expérimentations *in situ* et au laboratoire les réponses structurelles et fonctionnelles de ces communautés à divers scénarios de changement climatique. Une attention particulière a été portée sur l'impact de la température et des précipitations sur la physiologie et le comportement d'espèces clefs, et sur les interactions trophiques au sein des communautés.

En dépit d'un renouvellement important des espèces d'invertébrés entre localités, les principales fonctions écosystémiques (*e.g.,* décomposition) sont assurées de façon constante par un cœur densément connecté de détritivores et de micro-organismes. Ce cœur fonctionnel est présent sur l'ensemble de l'aire de distribution des broméliacées à réservoirs, et alimenté par la chute de litière et de cadavres d'invertébrés terrestres. La dynamique des populations et des communautés s'est révélée plus stable que supposé face aux perturbations appliquées dans ces travaux. Cette stabilité est conférée par les caractéristiques morphologiques de la plante hôte qui tamponnent les fluctuations environnementales, par les différents traits de résistances des espèces d'invertébrés, et par la ségrégation spatio-temporelle des niches des espèces.

Ces différentes approches empiriques et expérimentales ont permis de mettre en évidence des interactions entre les changements environnementaux et la réponse des communautés qui soient indépendantes des échelles spatiales considérées et qui sembleraient communes à divers écosystèmes de plus grandes tailles.

Mots-clefs: changements environnementaux; hétérogénéité des habitats; forêts néotropicales; stabilité; réseaux trophiques; macroinvertébrés; broméliacées à réservoirs; diversité spécifique; fonctionnement des écosystèmes; traits fonctionnels; échelle spatiale locale à régionale

ABSTRACT

Neotropical forests shelter an astonishing and underrated biodiversity. The integrity and stability of these natural ecosystems are threatened by human-induced environmental changes. Therefore, highlighting the determinants of ecosystem functioning, be they natural or anthropogenic, is a daunting but paramount scientific challenge. The intrinsic complexity of highly diversified ecosystems arouses both conceptual and logistical difficulties, which we handle, by manipulating tiny ecosystems, the tank bromeliads. The leaves of tank bromeliads form wells that hold rainwater and intercept leaf litter, allowing for a simple invertebrate aquatic community to thrive. These plants can be exhaustively sampled, are naturally replicated, and widely distributed.

From local to biogeographic scales, this thesis aims at understanding how these communities respond to the natural heterogeneity of Amazonian forests, and at predicting the impacts of human-induced disturbances on the structure and functioning of these communities, using *in situ* and lab experiments. Particular focus is attributed to the influence of some aspects of climate changes (*e.g.,* warming, and various precipitations scenarios) on individual physiology, behavior, and trophic interactions.

Despite a high turnover in invertebrate species composition across localities (influence of local factors and historical processes), main ecosystem functions were consistently ensured by a densely interconnected core of detritivores and microorganisms. This functional core was found in all studied localities and unceasingly fueled by leaf litter and terrestrial invertebrate carcasses. Regarding the disturbances we applied, the dynamics of populations and communities were more stable than expected. This stability is conferred by the morphology of the host plant, the resistance traits of aquatic invertebrates and the spatial-temporal segregation of species niches, which altogether buffered fluctuations in environmental conditions.

The various empirical and manipulative approaches used in this thesis have highlighted interactions between environmental changes and the responses of communities that are independent of the spatial scales considered and may be shared by several ecosystems varying in size.

Keywords: environmental changes; habitat heterogeneity; neotropical forests; stability; trophic networks; macroinvertebrates; tank bromeliads; species diversity; ecosystem functioning; functional traits; from local to continental scale

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“*Novelties come from previously unseen association of old material.*
To create is to recombine”

Jacob 1977

En ce sens, la vie, l’art, et les sciences ont beaucoup en commun :
118 éléments chimiques ; 4000 minéraux ; 1 300 000 espèces ; 110 600 000 articles.
3 couleurs primaires ; combien de tableaux ?
7 notes de musique ; combien de chansons ?

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INTRODUCTION

La sixième extinction de masse serait engagée **(Ceballos *et al.* 2015)**. Les activités anthropiques sont à l'origine de l'érosion de la biodiversité, de la diversité des gènes, des espèces, des communautés, au fonctionnement des écosystèmes **(Barnosky *et al.* 2011, Fey *et al.* 2015)**. En comparaison, l'activité géologique (notamment le volcanisme), solaire, et/ou les impacts de météorites semblent être les principaux facteurs des cinq extinctions de masse précédentes. Cependant, pour chacune d'elles, l'importance relative de ces différents facteurs et leurs conséquences exactes restent hypothétiques, faute de séquences complètes de fossiles. L'étude de ces six différents évènements catastrophiques souligne le lien intime entre la biodiversité et nombre de facteurs environnementaux, plaçant ainsi le rôle des changements locaux à globaux, qu'ils soient d'origine naturelle ou anthropique, au centre de l'attention des écologues. Au-delà des services écosystémiques que la biodiversité dispense à la société, en termes de cycle de l'eau et du carbone, et de sources de produits alimentaires et thérapeutiques, les millions d'années d'évolution lui ont conféré une valeur esthétique inestimable. La vitesse à laquelle cette sixième extinction influence la biodiversité accentue l'urgence de comprendre les mécanismes d'assemblage (et de désassemblage) des communautés, de déterminer comment ces mécanismes changent de l'échelle locale à l'échelle biogéographique, afin de prédire les conséquences de ces changements sur les fonctions et services écosystémiques dont l'homme dépend.

1 Les changements environnementaux et leurs conséquences sur les organismes

Les changements environnementaux regroupent une multitude de facteurs dont les conséquences sont visibles à toutes les échelles biotiques, spatiales et temporelles. Les impacts, directs et/ou indirects, de l'activité humaine se déclinent en quatre grandes catégories: i) la destruction ou surexploitation des habitats et des stocks, ii) les pollutions conduisant à l'eutrophisation des habitats et/ou le rejet des déchets toxiques, iii) l'introduction d'espèces exotiques, et iv) le changement climatique. Les travaux de cette thèse se concentrent sur l'impact de certains aspects du changement climatique.

1.1 Les conséquences acceptées du changement climatique

Le réchauffement de l'atmosphère, imputable au rejet de gaz à effet de serre dont le dioxyde de carbone (activité industrielle, particuliers, déforestation), est une source de dérèglement climatique **(IPCC 2013)**. Les prédictions alarmantes pour la période 2000-2100 ont déjà identifié des aires géographiques particulièrement vulnérables comme le bassin Amazonien, l'Afrique de l'ouest, le Sahel, le plateau du Tibet, et l'Indonésie (Figure I.1; **Diffenbaugh & Giorgi 2012**). Une première conséquence de l'augmentation de la température est la modification de l'aire de distribution géographique des espèces **(Walther *et al.* 2002, Parmesan 2006, Rahel *et al.* 2008, Rahel & Olden 2008)**. Les aires de distribution diminuent, s'agrandissent et/ou se déplacent vers les pôles où les conditions abiotiques deviennent plus optimales. Ces déplacements vers les hautes latitudes peuvent aussi s'accompagner de mouvements vers les hautes altitudes **(Rabasa *et al.* 2013)**. Les modifications des aires de répartition de certaines espèces ne sont pas sans conséquences puisqu'elles peuvent conduire à de nouvelles interactions biotiques (compétition, prédation) avec les espèces déjà présentes **(Van der Putten *et al.* 2010)**. Ainsi, aux contraintes thermiques viennent s'ajouter des modifications des patrons d'interactions ou contraintes biotiques avec les espèces en mouvement **(Montoya & Raffaelli 2010)**.

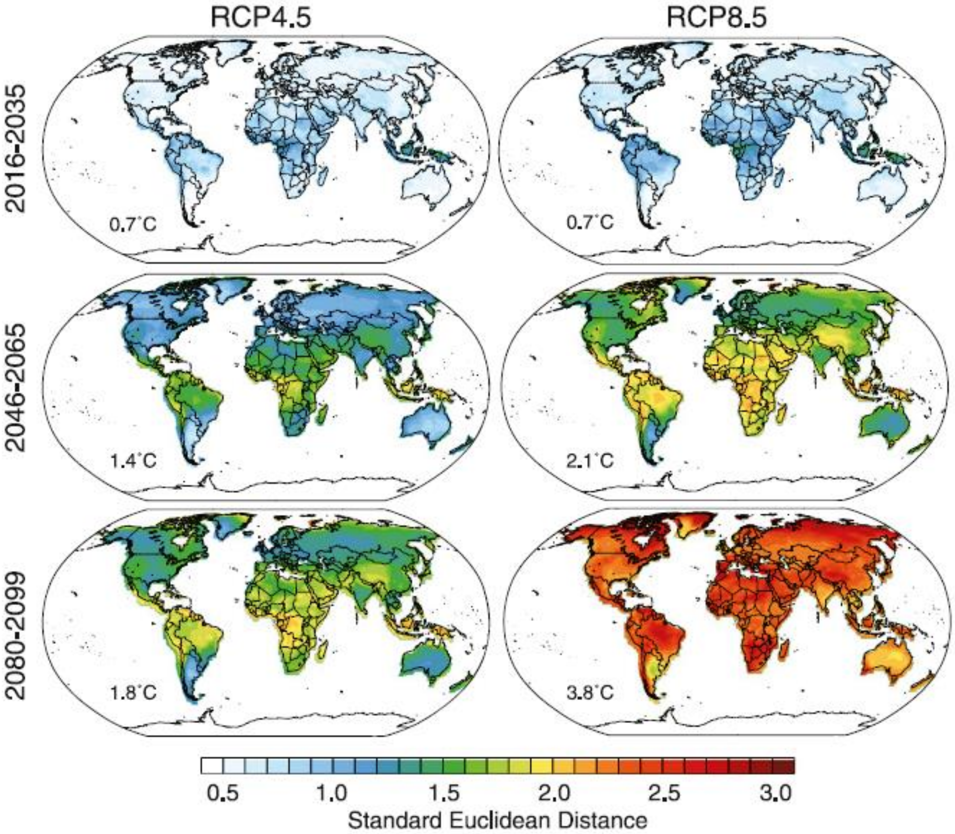

Figure I.1 Prédictions des variations de l'indice de changement climatique, calculé à partir de la distance euclidienne standard, et de 7 indicateurs climatiques mesurés au cours de 4 saisons sur la période 1986-2005. Ces prédictions sont basées sur deux scénarios climatiques de rejets de gaz à effets de serre (RCP4.5 et RCP8.5), et portent sur les périodes de 2016-2035, 2046-2065, et 2080-2099. Les températures présentées dans le coin en bas à gauche, représentent les médianes des températures globales au-dessus de la ligne de base du 20ème siècle. Cette figure provident de l'article de **Diffenbaugh & Giorgi (2012)**.

Une deuxième conséquence importante des dérèglements climatiques est un découplage de la dynamique temporelle des populations via la modification de la phénologie des espèces. Par exemple, une modification de la synchronisation de la floraison influence la relation entre plantes et pollinisateurs, un décalage du temps de réponse des plantes ligneuses aux fluctuations environnementales impacte l'assemblage d'oiseaux associés **(Kissling *et al.* 2010)**, et enfin ce même temps de réponse différentiel entre espèces découple la dynamique entre certains prédateurs et leurs proies **(Devictor *et al.* 2012)** ou certains parasites et leurs hôtes **(Møller *et al.* 2011)**. Ces problèmes de dislocation temporelle sont exacerbés par les temps de réponses différentielles des espèces, réduisant considérablement la fiabilité des prédictions issues d'études écologiques.

1.2 Les conséquences débattues et émergentes du changement climatique

La difficulté de trouver des réponses aux changements de température qui soient communes à une majorité d'espèces a poussé certains écologues à s'intéresser aux déterminants de la vitesse des réactions chimiques, ce qui a donné naissance à la théorie métabolique de l'écologie **(Kleiber 1932, Brown *et al.* 2004)**. Cette théorie stipule que l'activité et les contraintes énergétiques des organismes sont régies par la température, et qu'elles sont proportionnelles à la masse corporelle élevée à la puissance trois quarts. Cependant cette théorie reste controversée car certains organismes ne suivent pas cette règle (protistes et certains ectothermes), et du fait de l'inadéquation entre prédictions et observations concernant la relation positive entre gradients latitudinaux de température et taille du corps **(Hawkins *et al.* 2007)**. La température peut interagir avec la nutrition de façon complexe en exacerbant la difficulté de discriminer clairement une réponse de la taille du corps à des variations des conditions thermiques **(Ozgul *et al.* 2010, Gardner *et al.* 2011, Meiri 2011)**.

Finalement, une conséquence mal connue de l'accroissement des températures est l'augmentation de la fréquence et de l'intensité des phénomènes climatiques extrêmes **(IPCC 2013, Knapp *et al.* 2015)**. Par exemple, la fréquence des sécheresses a augmenté en Méditerranée depuis 1950 **(Spinoni *et al.* 2015)**. Si l'augmentation des sécheresses peut paraître inquiétante, certaines études ont démontré qu'elles n'avaient que peu d'influence sur le maintien d'importantes fonctions écosystémiques (*e.g.,* la productivité). En effet les rares évènements de précipitations extrêmes viendraient contrebalancer l'impact négatif de ces sécheresses **(Cherwin & Knapp 2012)**. Comprendre comment ces évènements extrêmes impactent les communautés écologiques, permettrait donc d'affiner les prédictions des effets d'un climat continuellement changeant. Les effets des perturbations d'origine anthropique, des dérèglements climatiques en particulier viennent ainsi modifier la physiologie et le comportement des organismes. Ces modifications engendrent des dislocations spatio-temporelles des patrons d'interactions avec comme conséquence majeure, l'émergence de nouvelles communautés **(Montoya & Raffaelli 2010)**.

2 Structure et stabilité des communautés écologiques face aux perturbations

Les changements environnementaux affectent *directement* les organismes vivants en modifiant leur physiologie, leur métabolisme, et leur comportement, et *indirectement* via une modification des réseaux d'interactions (Encadré 1). L'étude *in situ* et *ex situ* de la structure et de la stabilité des réseaux d'interactions a permis de mettre en exergue certaines propriétés leur permettant de faire face à ces changements.

Encadré 1 : Les communautés écologiques

Si la propension de la vie ou des espèces est de se multiplier, cela passe avant tout par la survie dans un habitat donné, et par la recherche d'une source d'énergie. Dans un monde fini, les ressources, habitat et énergie, sont limitantes. En ce sens, une communauté écologique est définie comme un ensemble d'espèces partageant des ressources communes. Dans les communautés, les espèces ne sont pas isolées. Il existe trois principaux types d'interactions, définis selon les coûts et bénéfices, en terme de valeur sélective (croissance, survie, succès reproducteur), pour les protagonistes impliqués dans l'interaction: la compétition (-/-), le mutualisme (+/+), et les relations trophiques (+/-). Les mécanismes d'assemblage des communautés et de coexistence d'espèces sont principalement issus de l'étude d'espèces interagissant par compétition **(Ackerly 2003, Gotzenberger *et al.* 2012)**, alors que les réseaux trophiques étaient le centre d'intérêt d'écologues plus soucieux de l'aspect fonctionnel des communautés au travers du transfert d'énergie entre individus le long des chaînes trophiques **(Elton 1927, Fausch *et al.* 2002)**. Les relations mutualistes ont été principalement étudiées en isolation. Cependant, suite à la reconnaissance de structures comparables entre ces différents types de réseaux d'interaction **(Kondoh *et al.* 2010, Thébault & Fontaine 2010)** on observe une volonté croissante des écologues de mettre en évidence des similarités dans les mécanismes sous-jacents, comme le filtrage environnemental, la dispersion, et la stochasticité **(Massol 2008, Vellend 2010)**.

2.1 La structure des réseaux trophiques

Un réseau trophique est un ensemble d'espèces (formant des « nœuds ») reliées par des « liens » (interactions proies-prédateurs) et agencées en niveaux trophiques, des producteurs primaires aux prédateurs (Figure I.2). Ces niveaux s'influencent mutuellement par le biais de cascades trophiques (que les effets soient descendants ou ascendants) qui contrôlent l'abondance et la biomasse des espèces. Cependant, la notion de niveau trophique ne reflète que partiellement la réalité biologique du fait de la complexité des réseaux qui incluent les boucles trophiques, de multiples chaînes alimentaires, et du fait qu'un prédateur peut prélever des proies à différents niveaux.

La complexité de la structure topologique des réseaux est positivement corrélée à la richesse spécifique ou diversité taxonomique **(McCann 2000)** et s'exprime aussi via la distribution des interactions/liens entre ces espèces. Deux indices principaux permettent d'estimer cette distribution: la densité de liens correspond au nombre moyen de liens par espèce, et la connectance qui représente le nombre de liens réalisés par rapport au nombre de liens potentiels. D'autres indices sont utilisés pour apporter des informations complémentaires comme, par exemple, l'emboîtement qui est un proxy du degré de partage des interactions et la modularité qui représente le degré de compartimentation des réseaux **(Thébault & Fontaine 2010)**. A l'évaluation qualitative de la structure du réseau peut s'ajouter la quantification du rôle des espèces dans la communauté. En pondérant par exemple les nœuds par l'abondance, la biomasse, et/ou la productivité des espèces, la taille des nœuds devient alors proportionnelle à l'importance fonctionnelle des espèces **(Whittaker 1965, Grime 1998)**. De même, certains écologues mesurent la force de l'interaction entre deux espèces en intégrant ses variations dans la représentation des réseaux **(Paine 1980)**.

2.2 Cette structure est-elle stable ?

Conjointement à l'étude qualitative et quantitative de la structure des réseaux trophiques, s'est posée la question de la relation entre structure/complexité et stabilité des réseaux. Du point de vue des mathématiques, une des définitions de la stabilité stipule qu'une communauté est stable si la part réelle des valeurs propres de la matrice associée (espèces *x* espèces) est négative, traduisant ainsi un retour rapide à l'état d'équilibre après une perturbation **(McCann 2000, Ives & Carpenter 2007)**. En résumé, si on se réfère à la littérature, la stabilité d'un réseau peut être évaluée à partir de quatre propriétés mesurables principales: la résistance, la résilience, la persistance, et la variabilité. La résistance mesure la capacité d'un système à maintenir l'intégrité de ses propriétés face à une perturbation alors que la résilience traduit la vitesse à laquelle ce système retourne à l'état initial suivant l'arrêt de cette perturbation **(Holling 1973)**. Une communauté ou des populations sont persistantes si les fluctuations des effectifs n'atteignent pas le seuil critique de 0. Et enfin, à persistances égales, les populations dont les fluctuations temporelles des effectifs sont les plus variables seront moins stables **(McCann 2000)**.

Le lien entre structure/complexité/diversité et stabilité a longtemps été débattu **(May 1972, Yodzis 1981, McCann 2000, Allesina & Tang 2012)**. Ce débat a permis de faire émerger des propriétés générales des réseaux trophiques **(McCann 2000)**. Par exemple, la stabilité de systèmes complexes est maintenue par une distribution non-aléatoire des liens entre les espèces, par une asymétrie dans la force des interactions, et enfin par la présence d'un grand nombre d'interactions faibles (stabilisant) comparé au nombre d'interactions fortes (déstabilisant). En effet, comme un prédateur ne dépend pas exclusivement d'une seule espèce de proie, les variations d'abondances des proies auront peu d'importance sur la population du consommateur. Plus généralement, la connectance et la diversité semblent directement affecter la persistance et résilience des réseaux trophiques et indirectement via des changements de la compartimentation et de l'emboîtement (Figure I.2; **Thébault & Fontaine 2010**).

Bien plus que la richesse spécifique ou diversité taxonomique, la fonction des espèces dans l'écosystème est un meilleur prédicteur de la stabilité **(Loreau *et al.* 2001)**. D'après l'hypothèse de redondance fonctionnelle, une plus grande diversité taxonomique permettrait aussi de maintenir l'intégrité du fonctionnement d'un écosystème (résistance) suite à l'extinction locale d'une espèce (Figure I.2). L'effet de la redondance fonctionnelle est, néanmoins, modulé par le processus écosystémique en question, et le nombre et l'importance relative des espèces dans le groupe fonctionnel **(Rosenfeld 2002, Petersen *et al.* 2003)**. Mais de façon générale, l'augmentation de la diversité taxonomique augmente le nombre de fonctions dans le système **(Hooper *et al.* 2005, Lefcheck *et al.* 2015)**. Par exemple, la forte productivité de systèmes diversifiés, via une meilleure exploitation des ressources disponibles, permet une meilleure résistance **(Isbell *et al.* 2015)** et résilience à une perturbation que ce soient en milieux terrestres **(Tilman 1982, Moore *et al.* 1993, Mylius *et al.* 2001)** ou aquatiques **(Downing & Leibold 2010, Downing *et al.* 2012)**.

2.3 Aspects dynamiques de la stabilité et des perturbations associées

Les changements plastiques de la prédation suite à la diminution locale de l'abondance d'une proie permettent d'accroître la stabilité du reste du réseau **(Kondoh 2003)**. En ce sens, la structure n'est plus une entité statique mais dynamique où les liens peuvent se créer et se défaire au fil du temps. Si un prédateur consomme plusieurs proies, la rareté de l'une d'elles entraîne une plus forte pression de prédation sur l'autre permettant la coexistence/persistance des deux proies dans le temps. Cette observation a fortement contribué au concept d'« espèces clefs de voûte » et du rôle prépondérant et structurant des prédateurs à l'apex du réseau **(Paine 1963)**. Toujours d'un point de vue dynamique et à l'échelle de la communauté, une forte richesse spécifique permet une réponse différentielle des espèces qui la composent face à une perturbation commune via l'effet portfolio **(Doak *et al.* 1998)**. Dans une communauté diversifiée, les dynamiques des populations peuvent ainsi être variables, donc instables, mais les fluctuations de la moyenne des dynamiques s'atténuent grâce à l'effet stabilisant de la covariance négative **(Doak *et al.* 1998)**.

Jusqu'à maintenant nous avons vu que la définition de la stabilité n'est pas triviale, car elle englobe plusieurs aspects et s'exprime à toutes les échelles biologiques, du comportement des organismes, à la structure et au fonctionnement des communautés en passant par la dynamique des populations. Un élément indissociable de la stabilité est la définition d'une perturbation. Une perturbation écologique est un changement brutal mais temporaire des conditions environnementales conduisant à l'extirpation d'une partie de la biomasse du système. A l'inverse, la définition du stress reflète un changement graduel dans les conditions environnementales et induit une baisse de performance des individus, sur le plan physiologique **(White *et al.* 1999)**.

Si l'intensité et la durée d'une perturbation ou d'un stress sont facilement concevables et donc mesurables (*e.g.,* biomasse extirpée, réduction de la performance, nombre de jours), la prise en compte de leur caractère dynamique, à travers leur fréquence, est une tâche nettement plus difficile à appréhender. Cette appréhension s'exprime dans le débat autour de l'hypothèse de perturbations intermédiaires dont les prédictions supposent que la diversité est maximisée dans un environnement où la fréquence/intensité des perturbations est modérée. De nombreuses études ont démontré une relation entre diversité taxonomique et perturbations dont le signe varie mais tend à être négatif **(Randall Hughes *et al.* 2007)**. Dans ce cadre théorique, une perturbation est une cause de changement de diversité mais si les espèces sont adaptées à un régime de perturbation particulier alors ce régime n'est plus une cause externe mais une propriété intrinsèque du système. Ce régime de perturbations peut alors faire partie des fluctuations naturelles de l'environnement et s'apparenter à un processus déterministe comme le filtrage environnemental (théorie du modèle de l'habitat; **Grime 1977, Southwood 1977, Korfiatis & Stamou 1999**). Par exemple, les espèces pionnières ou à stratégies rudérale ont besoin d'un certain régime de perturbation pour se maintenir dans la communauté, de même que les invertébrés aquatiques de milieux temporaires sont adaptés aux assèchements fréquents **(Dolédec *et al.* 2006, Sim *et al.* 2013)**.

Perturbations et stress varient, en intensité, durée, fréquence, et spécificité (espèce, stade de vie, et/ou localité touchée; **White *et al.* 1999**), mais peuvent se placer sous le terme plus général de « contraintes ». Ces contraintes fluctuent dans le temps et dans l'espace et peuvent être qualifiées de naturelles ou anthropiques selon leur origine. Il existe cependant un seuil à partir duquel les communautés n'arrivent plus à suivre le rythme des changements de ces fluctuations. Pléthore de termes existe autour de cette notion de seuil: changement de régime; effet d'hystérésis; seuil écologique; transition critique; effondrement catastrophique; point de basculement; équilibre alternatif; état alternatif stable; ralentissement critique **(Scheffer *et al.* 2001, Scheffer & Carpenter 2003, Scheffer *et al.* 2012, Ratajczak *et al.* 2014, Villa Martín *et al.* 2015)**. Tous ces termes soulignent le difficile retour à l'état initial après, ou juste avant, avoir atteint un seuil critique dans les changements (d'origine naturelle ou anthropique) des conditions environnementales abiotiques et/ou biotiques. Un des défis écologiques contemporain est peut-être d'arriver à détecter ces seuils avant qu'ils ne soient franchis. Ainsi, l'étude des milieux mal connus et/ou encore peu impactés par l'Homme semble une priorité.

3 Les forêts tropicales: une diversité méconnue et menacée

Les forêts tropicales accueillent une fraction importante de la biodiversité terrestre. De nombreuses études s'attèlent à la description de cette biodiversité méconnue et tentent de définir les facteurs qui déterminent son fonctionnement. Une des hypothèses est que l'hétérogénéité spatiale et temporelle naturelle des habitats (par exemple, l'ouverture des milieux, les fluctuations climatiques saisonnières, et feux naturels) joue un rôle structurant clé. A cette hétérogénéité se surimpose l'impact des changements environnementaux. Dans ce contexte, les écologues tentent de relier la réponse des organismes et des communautés des forêts tropicales à l'hétérogénéité des habitats et aux perturbations d'origine anthropique.

3.1 Une forte diversité en lien avec une hétérogénéité naturelle des habitats

On estime que les arthropodes représentent 78.5% de la diversité spécifique planétaire **(Zhang 2013)** et que 50 à 75% de la totalité des espèces terrestres vivent au sein des forêts tropicales **(Tuomisto *et al.* 1995, Myers *et al.* 2000)**. Parmi ces espèces terrestres tropicales, les arthropodes représenteraient 94% de la biomasse totale **(Fittkau & Klinge 1973)**. Ces estimations tendent à devenir plus précises grâce à la multiplication des études scientifiques et des protocoles d'échantillonnage plus structurés **(Samways 2007, Hamilton *et al.* 2010, Basset *et al.* 2012)**. Cependant, une importante fraction de la diversité spécifique reste à découvrir **(Mora *et al.* 2011)**, ainsi que les informations bio-écologiques de base (traits fonctionnels; **Godfray *et al.* 1999**) et les causes d'une telle diversité.

De l'échelle locale à régionale ou biogéographique, cette diversité spécifique est distribuée de façon hétérogène **(Rahbek 2005, Fahr & Kalko 2011)**. L'hypothèse de l'hétérogénéité des habitats **(Simpson 1949)** suppose que la complexité structurelle des habitats augmente la disponibilité des niches potentielles et permet la colonisation et le maintien d'une importante diversité spécifique (voir la synthèse bibliographique de **Tews *et al.* 2004**). En d'autres termes, cette hétérogénéité favorise la spécialisation et l'évitement de la compétition grâce à la ségrégation spatiale de l'utilisation des ressources.

Cette hypothèse a été préférentiellement testée dans des milieux anthropisés **(Tews *et al.* 2004)**, oubliant, de fait, l'hétérogénéité naturelle des habitats **(Willig *et al.* 2003, Willig *et al.* 2011)**. Dans les forêts tropicales, cette hétérogénéité se traduit, notamment, par un gradient de complexité lié à l'ouverture/fermeture du milieu et à l'exposition au soleil **(Cardoso *et al.* 2010)**. On trouve, par exemple rien que pour la Guyane française de nombreux habitats naturels tels que savanes, forêts de bas-fonds, de terre ferme, forêts de lianes pour ne citer qu'eux **(Guitet *et al.* 2015)**. Selon la structure et la composition du couvert végétal, les communautés d'arthropodes herbivores et détritivores changent via, notamment, des variations de la palatabilité des feuilles vivantes et mortes **(Hättenschwiler & Gasser 2005)**.

Cette hétérogénéité se traduit aussi par l'occurrence de certains phénomènes climatiques qui oscillent naturellement comme les cycles El Niño-La Niña. Ces oscillations induisent la succession de périodes de sécheresse et d'intenses précipitations vers la côte Pacifique de l'Amérique latine ayant une influence démontrée, par exemple, sur des communautés d'hyménoptères en Guyane Française **(Dejean *et al.* 2011)**. Cette ségrégation spatiale de l'utilisation des ressources peut donc s'accompagner d'une ségrégation temporelle en lien avec les fluctuations climatiques naturelles. Les climats tropicaux, contrairement à leurs homologues tempérés, sont caractérisés par de faibles fluctuations annuelles de températures mais d'importants changements des régimes de précipitations. Si l'influence des variations climatiques sur les communautés est relativement bien documentée en milieux tempérés, la réponse des communautés tropicales à ces variations est moins connue.

3.2 Une hétérogénéité naturelle en interaction avec les changements environnementaux

L'étude des paléoclimats (Pleistocène) indique que la biodiversité des forêts tropicales a été moins touchée par les glaciations que celle des forêts tempérées grâce à la persistance de milieux refuges **(Haffer & Prance 2001, Bush & Oliveira 2006)**. Depuis plusieurs années, ces forêts tropicales sont fragilisées par les changements d'utilisation des terres **(Phillips *et al.* 2009)**, la déforestation **(Laurance 2005)**, l'introduction d'espèces exotiques **(Fujita *et al.* 2014)** ou encore les modifications climatiques **(Lewis *et al.* 2011)**. A ce jour, près de 50% de la surface historique des forêts tropicales a disparu **(Wright 2005)** avec des conséquences quasi irréversibles sur la diversité biologique. Même si moins visible, le réchauffement climatique est pointé du doigt pour expliquer la réduction de la richesse spécifique des plantes vasculaires en Guyane française **(Fonty *et al.* 2009)**. Les températures en milieux tropicaux sont plus hautes que celles des milieux tempérés et seraient déjà proches de l'optimum thermique de plusieurs espèces tropicales **(Tewksbury *et al.* 2008)**. Cependant, les prédictions du climat sur le bassin Amazonien en particulier sont variables (Figure I.1). La côte Nord-Est de l'Amérique du sud et l'Amérique Centrale sont supposées s'assécher alors que les côtes sud-est de l'Amérique du sud pourraient subir de fortes précipitations **(Karmalkar *et al.* 2008, Magrin *et al.* 2014)**.

Ces changements climatiques peuvent donc interagir avec l'hétérogénéité naturelle des habitats. On peut alors se demander comment des communautés animales ou végétales présentes dans des forêts primaires répondraient à différents scénarios de précipitation. Est-ce que des communautés présentes en milieux exposés au soleil et sous couverts forestiers répondraient similairement ou différemment à un même évènement climatique ? Il devient donc urgent de comprendre comment les communautés tropicales répondent à l'hétérogénéité naturelle des habitats et à un changement des conditions environnementales induit par les activités anthropiques.

3.3 Des écosystèmes diversifiés, et complexes, difficiles à étudier

Comprendre comment les communautés et les écosystèmes répondraient à des perturbations environnementales est très complexe. En effet, l'étude et la manipulation expérimentale d'écosystèmes diversifiés représente un défi technique rarement réalisable pour trois principales raisons, i) la complexité inhérente de ces systèmes, ii) la difficulté de répliquer les expériences/observations, et iii) la longueur du temps de réponse des macro-écosystèmes face à une perturbation donnée.

Premièrement, l'échantillonnage exhaustif « idéal » de la communauté est quasi impossible dans des écosystèmes complexes caractérisés par une importante richesse spécifique grandement méconnue et dont les limites physiques sont incertaines (milieux terrestres continus *versus* milieux aquatiques bien délimités). De plus, l'évaluation de la diversité fonctionnelle via l'étude des traits fonctionnels (*e.g.*, régimes alimentaires, type de respiration, mode de reproduction) de chacune des espèces est d'autant plus laborieuse que le système est complexe. Deuxièmement, le nombre d'échantillons nécessaire à un traitement statistique robuste est difficilement atteint dans des macro-écosystèmes, empêchant ainsi, la mise en place de lots témoins et manipulés. Troisièmement, les temps de réponse de ces systèmes, et des organismes qui les composent, à certains évènements climatiques extrêmes peuvent s'étendre sur plusieurs années, un constat inquiétant face à la vitesse des changements environnementaux contemporains. Actuellement, notre connaissance de l'effet de certains aspects des changements environnementaux comme la sécheresse ou une augmentation du régime de précipitation est extrapolée à partir du suivi et de l'étude des milieux aquatiques temporaires **(Reznickova *et al.* 2007, Sim *et al.* 2013, Brendonck *et al.* 2015)** et/ou des milieux dont l'hydrologie est régulièrement influencée par des précipitations intenses **(Leung *et al.* 2012)**.

Pour pallier l'ensemble de ces difficultés les microcosmes de laboratoire offrent une alternative méthodologique intéressante bien que non dénuée de critiques. Sans s'étendre sur la relation tripartite, entre généralité, précision, et réalisme, proposée par **Richard Levins (1966)**, qui conditionne tous protocoles d'échantillonnage et manipulations expérimentales, un compromis prometteur pour mener des études empiriques et tester des hypothèses théoriques par l'expérimentation est l'utilisation des microcosmes naturels **(Srivastava *et al.* 2004)**. Parmi ces microcosmes naturels, nous nous intéressons dans cette thèse aux broméliacées à réservoir d'eau, des plantes à fleurs dont les feuilles agencées en rosette abritent un écosystème aquatique miniature.

4 Des modèles adéquats pour comprendre l'influence des changements environnementaux

Les broméliacées à réservoirs d'eau, en plus de pouvoir être échantillonnées de manière exhaustive, de supporter des réseaux trophiques aquatiques simples, et d'avoir une forte abondance locale, sont présentes sur une large aire de répartition. De plus, les temps de génération des espèces qui les habitent sont courts, une caractéristique essentielle à l'observation d'une réponse lors de manipulations expérimentales.

4.1 Les broméliacées à réservoirs

La famille des broméliacées est constituée de 3140 espèces reparties en 58 genres **(Givnish *et al.* 2011)**. Ce sont des angiospermes monocotylédones dont le centre de radiation évolutive, situé au niveau du bouclier des Guyanes, est daté de 100 millions d'années. Les lignées actuelles ont commencé à diverger et se répandre il y a 10-20 Millions d'années pour coloniser l'ensemble de leur aire de répartition, atteignant les régions subtropicales du Sud de l'Amérique du Nord, les îles de la mer des Caraïbes, jusqu'aux frontières de la Patagonie. On notera aussi la dispersion relativement récente (9,3 millions d'années) de *Pitcairnia feliciana* vers la partie tropicale de l'Afrique de l'Ouest **(Givnish *et al.* 2011)**.

Près de la moitié des espèces de cette famille présentent un réservoir d'eau ou "phytotelme" **(Benzing 2000)**. Les broméliacées à réservoirs doivent leur nom à la disposition de leurs feuilles formant une rosette. La base de chaque feuille forme un réservoir permettant l'accumulation d'eau (précipitations, condensation) et de litière provenant de la canopée (feuilles mortes, brindilles, graines, fleurs; **Richardson 1999, Benzing 2000, Armbruster *et al.* 2002, Srivastava 2006, Jabiol *et al.* 2009)**. Ces réservoirs foliaires qui communiquent de façon complexe peuvent contenir de quelques millilitres d'eau (*e.g., Tillandsia adpressiflora*) jusqu'à plusieurs litres d'eau pour les grosses plantes (*e.g., Aechmea aquilega, Neoregelia cruenta*; Figure I.2A).

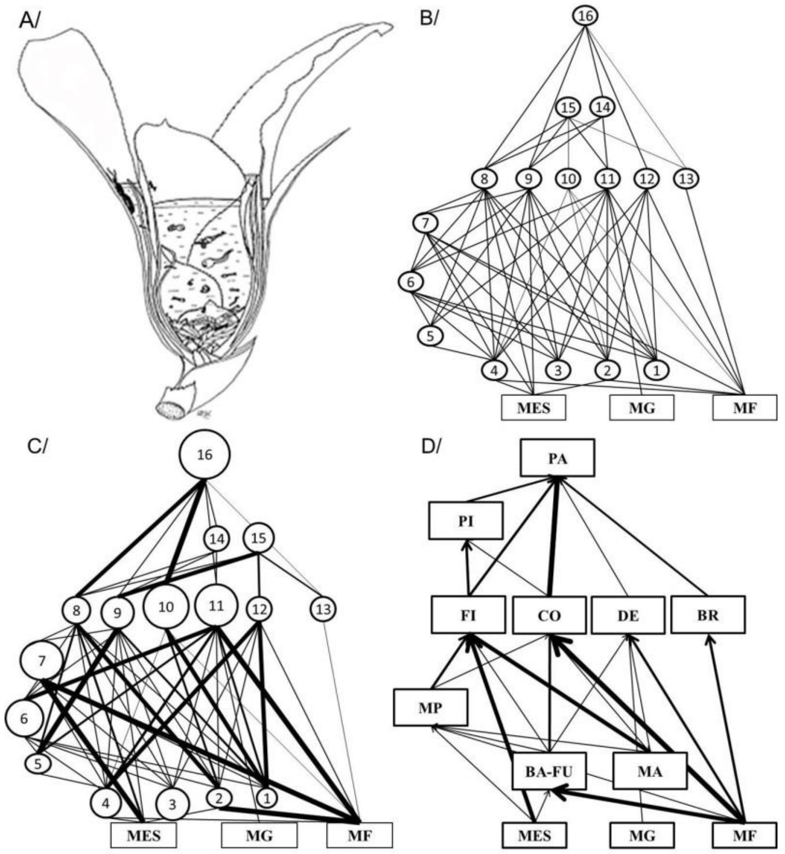

Figure I.2 A) Représentation schématique d'une coupe transversale d'une broméliacée à réservoirs **(Kitching 2000)**, *B) structure topologique ou « connectance web » d'un réseau trophique d'invertébrés aquatiques associés, C) structure quantitative d'un réseau trophique où les nœuds sont pondérés par l'abondance/biomasse, et les liens par la fréquence des interactions, et D) représentation quantitative des flux d'énergie entre les principaux compartiments fonctionnels. MES = matière en suspension, MG = matière grossière, MF = matière fine; espèces 1-7 = micro-organismes, espèces 8-13 = détritivores, espèces 14-15 = prédateurs intermédiaires, espèce 16 = prédateur à l'apex du réseau; MA = micro-organismes autotrophes, BA-FU = bactéries-fungi, MP = micro-organismes prédateurs, FI = filtreurs, CO = collectors, DE = déchiqueteurs, BR = brouteurs, PI = prédateurs intermédiaires, PA = prédateurs à l'apex.*

La matière organique détritique qui rentre dans les réservoirs constitue la principale source énergétique pour les organismes aquatiques et la plante elle-même. En effet, les broméliacées ont la particularité d'absorber l'eau et les éléments minéraux par des trichomes foliaires présents en grande densité à la base des feuilles directement en contact avec l'eau du réservoir (voir la synthèse de **Leroy *et al.* 2015** pour plus de détails). Ces caractéristiques morphologiques leur ont valu le nom de « marécages suspendus et fragmentés » ou de « saprophytes assistés » **(Picado 1913, Benzing 2000)**.

4.2 Les communautés d'invertébrés aquatiques

A la base du réseau trophique la source d'énergie est, en général, exclusivement détritique à travers la chute de litière. Toutefois, une étude récente a démontré l'importance du développement algal, chez des broméliacées exposées au soleil, celui-ci servant de ressource complémentaire pour le réseau trophique **(Brouard *et al.* 2012)**. La partie microbienne du réseau trophique constitue le premier maillon responsable de la décomposition de la matière organique. Ces agents microbiens, tels que bactéries et cyanobactéries **(Cochran-Stafira & von Ende 1998)**, champignons **(Brouard *et al.* 2012)**, protozoaires **(Carrias *et al.* 2001)**, rendent cette matière organique palatable pour les organismes des niveaux trophiques supérieurs.

Le maillon suivant est constitué des macroinvertébrés collecteurs (Chironomidae, Diptera), filtreurs (Culicidae, Diptera), brouteurs (Scirtidae, Coleoptera), et déchiqueteurs (Limoniidae, Diptera) qui se nourrissent de matière organique grossière ou fine, sédimentée ou en suspension, ainsi que des communautés microbiennes **(Frank & Lounibos 1983, Richardson 1999, Kitching 2000)**. Ces métazoaires détritivores sont ensuite consommés par les prédateurs (Chironomidae, et Corethrellidae, Diptera; Tabanidae et Culicidae, Diptera; Coenagrionidae, Odonata). Les abondances totales de ces métazoaires peuvent varier entre quelques individus à plusieurs milliers pour les broméliacées aux réservoirs les plus volumineux et la richesse spécifique varie, de 10 à 20 taxons par plante.

4.3 Les communautés terrestres gravitant autour des broméliacées

Ces écosystèmes miniatures sont également attractifs pour une faune terrestre diversifiée présente occasionnellement ou durablement **(Frank & Lounibos 2009)**. Certains amphibiens utilisent les réservoirs ponctuellement comme sites de ponte **(Poelman & Dicke 2008)**. Des œufs nourriciers sont généralement pondus par les femelles, et l'influence des têtards sur le réseau trophique d'invertébrés aquatiques reste encore à démontrer. Ces amphibiens et certains serpents et lézards agissent comme agents de dispersion (phorésie) d'invertébrés entièrement aquatiques comme les oligochètes et crustacés **(Lopez *et al.* 1999, Sabagh & Rocha 2014)**. Les amphibiens peuvent aussi se nourrir d'insectes venus trouver refuge ou chercher de la nourriture dans les réservoirs. Les blattes profitent aussi des broméliacées à réservoirs comme sites de ponte et de refuge aux micro-variations climatiques **(Frank & Lounibos 2009)**.

D'autres organismes sont présent durablement sur les broméliacées et sont impliqués dans une relation mutualiste. C'est le cas des araignées qui construisent des toiles au-dessus des réservoirs et qui capturent les insectes émergents **(Romero & Srivastava 2010, Hénaut *et al.* 2014)**. En jetant les carcasses d'insectes et leurs excréments dans les réservoirs d'eau, ces araignées participent à la nutrition minérale de la plante formant ainsi un mutualisme digestif **(Romero *et al.* 2006, Romero *et al.* 2008, Leroy *et al.* 2015)**. Les fourmis utilisent les broméliacées comme terrain de chasse ou site de nidification permanent. Certaines espèces nidifient directement dans les loges étanches ou réservoirs asséchés de certaines broméliacées **(Dejean & Olmsted 1997, Blüthgen *et al.* 2000, Talaga *et al.* 2015)** tandis que d'autres sont impliquées dans des relations plus étroite avec la formation des « jardins de fourmis » (voir la synthèse de **Orivel & Leroy 2011** pour plus de détails; Figure I.3). Ces fourmis en étroite relation avec les broméliacées vont indirectement modifier la structure spécifique et fonctionnelle des réseaux trophiques aquatiques présents dans les réservoirs d'eau **(Céréghino *et al.* 2011, Talaga *et al.* 2015)** eux même modifiant la nutrition de la plante **(Leroy *et al.* 2009, Leroy *et al.* 2013)**.

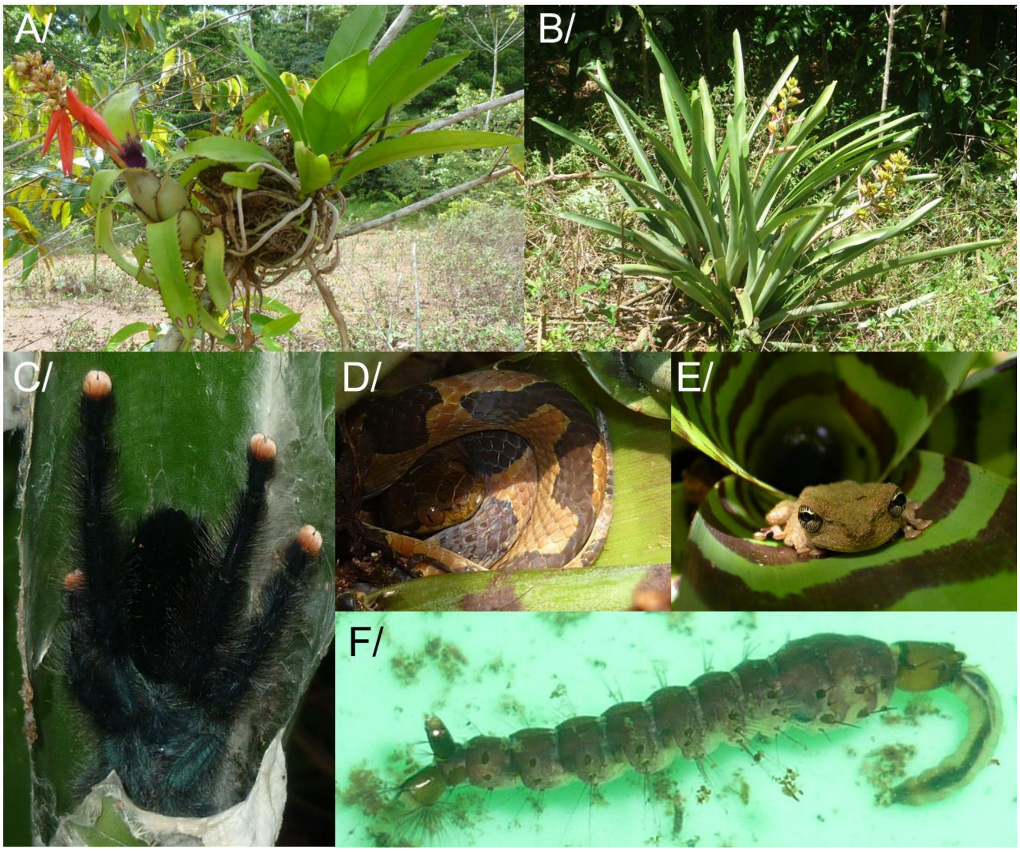

*Figure I.3 A) une broméliacée à réservoirs (*Aechmea mertensii*) présentes dans des jardins de fourmis, B)* Aechmea aquilega *se développant à terre en milieu exposé au soleil, C)* Avicularia avicularia *avec sa toile au-dessus du réservoir central d'une* Aechmea aquilega*, D)* Leptodeira annulata *au creux d'un réservoir de* Vriesea splendens*, E) Osteocephalus oophagus sur une* Vriesea splendens*, F) acte de prédation directe du vorace* Toxorhynchites haemorrhoidalis *sur une larve de Tipulidae (le prédateur utilisé dans le Chapitre 4). Photos: A et E = C. Leroy, B, C, D, et F = O. Dézerald.*

4.4 Limites de nos connaissances sur ce système

Le rôle des épiphytes dans le fonctionnement des forêts tropicales a longtemps été négligé **(Pittl *et al.* 2010)**. Certaines, de très grande taille, peuvent supporter, à elles-seules, une biomasse d'invertébrés terrestres supérieure à celle de l'ensemble de la canopée environnante **(Ellwood & Foster 2004)**. Parmi les épiphytes, le rôle des broméliacées à réservoir est méconnu. Leur densité peut pourtant varier entre 6000 (Chapitre 1) et 175000 individus par hectare **(Richardson 1999)** représentant plusieurs dizaines de milliers de litres d'eau et des centaines de kilogrammes de matière organique détritique **(Benzing 1990)**.

La diversité des communautés aquatiques est contrôlée par divers facteurs biotiques et abiotiques. Par exemple, la morphologie de la plante détermine la quantité d'eau interceptée, ainsi que la quantité de détritus entrants dans les réservoirs **(Jabiol *et al.* 2009)**. De plus, l'absorption des minéraux via les trichomes foliaires engendre le rejet d'ions d'hydrogène dans l'eau des réservoirs conduisant à acidifier le pH avoisinant 4.5 **(Laessle 1961, Richardson 1999, Lopez *et al.* 2009)**. Les micro-conditions environnementales des broméliacées à réservoir représentent un filtre pour la colonisation d'espèces spécialisées **(Marino *et al.* 2013)** et endémiques comparé aux conditions des milieux aquatiques environnants tels que les bractées d'*Heliconia* sp., les trous d'eau, ou autres réservoirs artificiels **(Yanoviak 2001a)**. Jusqu'à 140 espèces ou morpho-espèces ont été identifiées (base de données du Bromeliad Working Group), toutefois, de nombreux doutes subsistent encore quant à l'identification de groupes taxonomiques entiers comme certains diptères.

Si nos connaissances concernant l'écologie des broméliacées à réservoirs et de leurs communautés associées sont incomplètes, l'utilité de ces plantes comme modèle d'étude pour répondre à des questions théoriques n'est plus à démontrer **(Srivastava *et al.* 2004)**. La taille des plantes, le nombre de réservoirs, le volume d'eau et ses propriétés chimiques, la quantité de détritus et l'exposition au soleil, sont autant de filtres environnementaux qui influencent la distribution, l'abondance, et la richesse spécifiques des communautés d'invertébrés aquatiques **(Richardson *et al.* 2000a, Armbruster *et al.* 2002, Frank *et al.* 2004, Srivastava 2006, Jabiol *et al.* 2009, Montero *et al.* 2010)**. Les prédictions de la théorie biogéographique des îles **(MacArthur & Wilson 1967)** et de la métacommunauté **(Holyoak *et al.* 2005)** ont été testées, et les résultats démontrent que la taille de la métacommunauté influence significativement la composition spécifique et la diversité fonctionnelle **(Frank & Lounibos 1987, Richardson 1999, Trierweiler *et al.* 2005, Farjalla *et al.* 2012, LeCraw *et al.* 2014b)**. Et enfin, l'influence majeure des effets descendants a aussi été démontré sur la structure et le fonctionnement des écosystèmes **(Srivastava 2006, Srivastava & Bell 2009, Atwood *et al.* 2014, Hammill *et al.* 2015, Trzcinski *et al.* under revision)**.

Cependant, une des principales limites à l'étude de ce système est surement la généralité de la réponse des communautés à la variabilité naturelle ou aux perturbations anthropiques. En effet, la plupart des études citées ci-dessus se placent à une échelle spatiale locale, et ne relatent que partiellement le caractère dynamique de ce système. L'évaluation de cette réponse à l'échelle régionale ou continentale est limitée par le fort renouvellement de la composition spécifique entre localités, la difficulté de clairement identifier les espèces et leurs interactions, et la variabilité des efforts d'échantillonnage due à des contraintes logistiques **(Soberon 2007, Kissling *et al.* 2012)**. La biogéographie fonctionnelle offre alors une alternative prometteuse qui s'affranchit de la connaissance précise de chaque espèce, en utilisant une représentation schématique simplifiée mais quantifiable (*e.g.*, les traits fonctionnels) qui regroupe plutôt qu'elle ne dissocie les espèces d'une communauté **(Violle *et al.* 2014)**. Cette simplification permettrait ainsi de capturer les grandes tendances de la réponse des communautés à l'impact des changements environnementaux **(Chapin *et al.* 2000)**, comme par exemple, les effets des stress hydriques sur la tolérance physiologique des plantes de prairies **(Craine *et al.* 2013)**.

5 Objectifs et plan de thèse

Au cours de cette thèse je me suis concentré sur l'étude des réseaux trophiques pour l'aspect fonctionnel et intégrateur de ces interactions. Cette thèse se place au cœur des enjeux écologiques actuels, par l'étude d'un réseau d'interaction dans son ensemble, d'une échelle spatiale locale à une échelle régionale voire biogéographique, en utilisant une démarche empirique et expérimentale. Nos observations et expérimentations se sont déroulées en Guyane Française, dans une ou plusieurs localités selon l'échelle spatiale étudiée. Pour l'approche biogéographique, ces travaux ont profité d'une expérimentation menée le long d'un vaste gradient latitudinal (de Puerto Rico au Brésil) dans le cadre de collaborations internationales (Bromeliad Working Group).

Cette thèse a deux objectifs principaux:

(1) mettre en évidence et hiérarchiser les principaux déterminants biotiques et abiotiques de la structure et du fonctionnement de réseaux trophiques constitués par des communautés de macroinvertébrés néotropicaux aquatiques;

(2) dégager les facteurs et mécanismes de la stabilité de ces réseaux et écosystèmes en réponse à certains aspects du changement climatique, avec une attention particulière sur les effets des variations de températures et de précipitations.

Ces objectifs ont été abordés en deux parties distinctes:

PARTIE I: La première partie, déclinée en trois chapitres, documente la réponse des communautés aquatiques des broméliacées à réservoirs à l'hétérogénéité naturelle des habitats via l'accumulation de données empiriques à plusieurs échelles spatio-temporelles.

Chapitre 1: Tank bromeliads sustain high secondary production in a Neotropical rainforest (Dézerald *et al.*, soumis à *Ecology*)

Si les broméliacées à réservoirs sont des écosystèmes miniatures abritant des réseaux trophiques faunistiques, se posent alors les questions du renouvellement de la biomasse hétérotrophe dans ces systèmes, des principaux facteurs contrôlant cette dynamique, et par extension, des interactions entre « l'écosystème broméliacée » et la matrice terrestre environnante que constitue la forêt. Les estimations de la biomasse animale supportée par les épiphytes en forêt tropicale ont révélé des valeurs conséquentes **(Richardson *et al.* 2000b, Petermann *et al.* 2015)**, notamment par rapport à la biomasse d'invertébrés trouvée dans la canopée sus-jacente **(Ellwood & Foster 2004)**. Toutefois ces estimations représentent seulement des mesures “instantanées” qui ne rendent pas compte de la dynamique temporelle de la biomasse produite. Ce premier chapitre vise donc à quantifier la production secondaire (formation de biomasse par unité de temps par unité de surface) et la rapidité du renouvellement des populations d'invertébrés d'une espèce de broméliacée commune en Guyane, et tente d'extrapoler ces valeurs à l'échelle d'une parcelle de forêt. Nos prédictions supposent que l'abondance de la matière détritique à la base des réseaux trophiques, la relative stabilité des conditions climatiques inhérentes aux milieux tropicaux, et les traits fonctionnels permettant aux invertébrés de résister à ces fluctuations hydrologiques naturelles, permettraient aux broméliacées d'assurer une forte production secondaire malgré leur taille réduite.

Chapitre 2: Food-web structure in relation to environmental gradients and predator-prey ratios in tank-bromeliad ecosystems (Dézerald *et al.* 2013, *PloS One*, 8:e71735)

L’hétérogénéité spatio-temporelle des habitats sélectionne localement un groupe d’espèces selon leurs traits fonctionnels **(Simpson 1949)**. On peut alors se demander comment ce filtrage va influencer les patrons d’interactions trophiques. Les variations des propriétés topologiques (*e.g.,* richesse spécifique, distribution des liens) de ces réseaux trophiques le long de gradients environnementaux, à larges échelles spatiales, n’ont reçu que peu d’attention. Si la stabilité des réseaux trophiques est positivement corrélée à la complexité et à la diversité taxonomique **(McCann 2000)**, nous supposons que i) le désassemblage des réseaux trophiques le long de gradients environnementaux se ferait prioritairement par « le haut » (prédateurs) et par les espèces spécialistes, laissant place à un « cœur » densément connecté d’espèces généralistes (détritivores et microorganismes), ii) ce « cœur » assurerait les principaux processus écosystémiques (*e.g.,* décomposition), et iii) la stabilité du réseau serait menacée si ce « cœur » est impacté, ou si les espèces, qui le constituent, convergent dans leurs réponses aux variations des conditions environnementales. Pour tester ces prédictions, nous avons analysé les relations qui existent entre les propriétés topologiques d’un grand nombre de réseaux trophiques contenus dans les broméliacées à réservoirs (N=365) et les conditions environnementales locales dans cinq types d’habitats rencontrés en Guyane, de la forêt primaire à la forêt secondaire et à des plantations.

Chapitre 3: Are trophic pathways predictable across broad biogeographic scales? (Dézerald *et al.*, en préparation)

Les flux d’énergie le long des chaînes alimentaires sont déterminés par l’influence des effets descendants et ascendants via les top-prédateurs et la ressource à la base de la pyramide trophique, respectivement **(Wu *et al.* 2011)**. Localement, les conditions environnementales peuvent modifier l’importance relative de ces effets en contrôlant l’entrée des prédateurs dans le système ou en modifiant la quantité et la qualité de la ressource basale **(Kitching 2001)**. Par exemple, les réseaux trophiques des broméliacées présentent un transfert de dominance de la matière détritique à la base vers une matière constituée d’organismes autotrophes (algues) lorsqu’on passe de milieux fermés à ouverts **(Brouard *et al.* 2012)**. Ces effets sur la configuration des chaînes alimentaires sont-ils constants et prédictibles le long de gradients biogéographiques? Dans ce chapitre, nous étudions quantitativement, via les outils isotopiques, les variations de la force des effets top-down sur les principaux groupes fonctionnels des broméliacées, et dégageons la part de variation imputable aux gradients d’ouverture du milieu de celle due aux sites biogéographiques. Etant donné que le prédateur dominant (larves d’odonates) est une espèce généraliste et opportuniste nous supposons que i) les effets descendants seraient modulés par la composition spécifique des groupes fonctionnels donc dépendant du renouvellement biogéographique des espèces (variabilité intra-sites), mais que ii) l'ubiquité de certains groupes/espèces assurerait le maintien des flux d'énergie et des principaux processus écosystémiques (variabilité inter-sites). Cinq sites en Amérique latine ont été sélectionnés pour la comparaison des réseaux trophiques en milieux ouverts et fermés.

PARTIE II: Dans la deuxième partie, constituée également de trois chapitres, nous avons utilisé les propriétés des broméliacées à réservoirs (*e.g.*, petite taille, temps de réponse rapide) pour tester des hypothèses sur la réponse des communautés aquatiques et terrestres à certains aspects du changement climatique. La méthode utilisée est principalement l'expérimentation en laboratoire et en conditions naturelles.

Chapitre 4: Temperature:diet interactions affect survival through foraging behavior in a bromeliad-dwelling predator (Dézerald *et al.* 2015b, *Biotropica*, 47:569-578)

Dans un contexte de réchauffement climatique, il est difficile de savoir comment la température interagit avec le régime alimentaire pour influencer le comportement et la croissance des consommateurs **(Woodward *et al.* 2010a)**. L'objectif de ce chapitre est alors de comprendre les interactions entre des températures croissantes, un régime alimentaire contrasté; proies d'origine aquatique (larves de moustiques) *versus* proies d'origine terrestre (fourmis); et le comportement et le développement d'un prédateur situé à l'apex du réseau trophique, *Toxorhynchites haemorrhoidalis* (Diptera, Culicidae). Ce prédateur présente un intérêt supplémentaire pour son rôle en lutte biologique contre les vecteurs de maladies. D'après la théorie métabolique de l'écologie, une augmentation de la température induit une augmentation des contraintes énergétiques **(Brown *et al.* 2004)**. De plus, la théorie optimale de recherche alimentaire stipule qu'un consommateur faisant face à un choix devrait sélectionner la ressource nutritionnelle qui maximise le gain énergétique **(Mitra & Flynn 2005)**. Si un consommateur possède les traits morpho-anatomiques lui permettant de capturer efficacement la proie optimale, nous avons testé dans ce chapitre, l'hypothèse que la préférence pour une proie ne changerait pas avec une hausse de la température ambiante mais que la quantité d'individus ingérés augmenterait. Le protocole expérimental associe mesures *in situ* du régime alimentaire du prédateur, tests de choix, et développement des consommateurs en conditions contrôlées.

Chapitre 5: Functional trait responses of aquatic macroinvertebrates to simulated drought in a Neotropical bromeliad ecosystem (Dézerald *et al.* 2015a, *Freshwater Biology*, 60:1917-1929)

Nos connaissances de l'influence des sécheresses sur les communautés écologiques proviennent majoritairement de l'étude des écosystèmes des climats tempérés, comme par exemple les milieux aquatiques temporaires Méditerranéens et ceux arides d'Amérique du Nord **(Lake 2011)**. Les changements climatiques sont supposés altérer la prédictibilité et l'intensité de ces phénomènes hydrologiques naturels **(IPCC 2013, Boersma *et al.* 2014)**. Comment réagiraient des communautés tropicales à des réductions extrêmes et imprédictibles des précipitations? Si les combinaisons de traits fonctionnels reflètent un ensemble de conditions environnementales partagées par plusieurs espèces, on peut s'attendre à ce que les espèces d'un même système répondent de façon relativement synchrone (résistance ou déclin) à la sècheresse. On peut enfin penser que des conditions de sécheresse de plus en plus sévères mèneraient à une convergence progressive des traits fonctionnels représentés au sein des communautés. Dans ce chapitre, nous examinons la dynamique temporelle (pas de temps hebdomadaire) des assemblages de traits fonctionnels d'une communauté aquatique sous l'influence d'une sécheresse simulée qui triple la durée d'asséchement moyen du site d'étude considéré. La dynamique de recolonisation suivant l'arrêt de cette perturbation est également étudiée, et discutée au regard des sources de colonisateurs (résistance interne *vs* recolonisation depuis des patchs voisins).

Chapitre 6: Context-dependence in the response of Neotropical arthropods and amphibians to simulated precipitation regimes along a biogeographic gradient (Dézerald *et al.*, en préparation)

Les prédictions sur les changements climatiques suggèrent une augmentation de la fréquence et de l'intensité des évènements extrêmes, dont les occurrences seraient variables entre localités géographiques **(IPCC 2013)**. Néanmoins, ces changements de régimes de précipitations ne sont pas immédiatement ressentis par les communautés écologiques car les caractéristiques physiques des habitats (*e.g.*, taille, hydrologie) peuvent moduler / tamponner leurs effets **(Leuzinger & Koerner 2010)**. La plupart des études de l'influence des changements climatiques sur les communautés se situent à une échelle locale, et examine l'effet d'un seul scénario climatique. Dans ce dernier chapitre nous évaluons l'influence relative de facteurs abiotiques et biotiques, par le biais de différents traitements de précipitations, des caractéristiques de l'habitat, et des interactions biotiques, sur le comportement de sélection d'habitats par des organismes terrestres fonctionnellement importants (fourmis, araignées, et amphibiens). Cette expérience a été répétée dans trois sites d'étude en Amérique latine afin de déterminer si la réponse de ces organismes aux traitements appliqués est générale ou dépendante de la localité. Sachant que la composition spécifique change entre localités biogéographiques, on suppose que i) le signe et la magnitude de la réponse des organismes aux différents facteurs seraient variables entre localités, ii) les facteurs aux effets les plus importants seraient détectés quel que soit la localité. Si les facteurs abiotiques sont dominants alors les organismes sélectionneraient préférentiellement les traitements de précipitations modérément sévères ou ceux dont l'hydrologie est stable. Si les facteurs biotiques sont dominants, on s'attend à ce que les espèces changent leurs préférences environnementales pour des conditions moins favorables en présence d'espèces antagonistes.

Enfin, la discussion générale de cette thèse s'articule autour de cinq points: i) la réponse de la structure des communautés à l'hétérogénéité naturelle des habitats tropicaux, ii) l'influence des perturbations sur la stabilité des réseaux d'interactions trophiques, iii) une réflexion sur l'utilisation des différentes échelles d'étude (*e.g.,* biotique, spatiale, et temporelle) pour déterminer les causes des changements de patrons de diversité, iv) la possibilité de transposer ces résultats à des écosystèmes aquatiques de tailles différentes (*e.g.,* étangs, mares, rivières, lacs), et v) la proposition de perspectives de recherche.

PARTIE I

Chapitre 1: Tank bromeliads sustain high secondary production in a Neotropical rainforest

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Abstract. Epiphytes are keystone species in Neotropical rainforests and can host more animal biomass than the surrounding tree crowns, but the secondary production of these epiphytes, and the drivers behind the population dynamics of their associated invertebrates remain unknown. We studied the life histories and estimated the secondary production (from individual bromeliads to forest plots) of the aquatic invertebrates inhabiting a common tank bromeliad in French Guiana. Despite seasonal variations in precipitation, most species showed repeated growth patterns and overlapping cohorts throughout the year. Growth rates, cohort production intervals and production:biomass ratios correlated positively with functional traits that confer *in situ* resistance to drought. In addition to this "biological buffering" of environmental fluctuations, the secondary production of tank bromeliads is sustained by an abundant food supply (detritus), high ambient temperatures with low seasonal fluctuations, and the buffering capacities of the plant itself (water retention time, known as "physical buffering"). We estimated that an average, medium-sized bromeliad produces 8.96 g dry weight m^{-2} y^{-1}, a value that falls between the median values of 5.13 and 14.78 g DW m^{-2} y^{-1} for lakes and streams worldwide, respectively. More than 90% of the invertebrate production taking place in bromeliads is exported to the surrounding terrestrial environment through the emergence of amphibiotic insects that leave the plants as adults. Our estimates suggest that (i) secondary production is not directly related to the size of the system nor to species richness because the production within bromeliad ecosystems that contain only a few invertebrate species is comparable to some of the much larger ecosystems, and (ii) depending on their density, tank bromeliads may have a substantial impact on Neotropical forest food webs since newly emerged adults are subsequently preyed on by terrestrial predators.

Key words: Biomass turnover; population dynamics; invertebrates; epiphytes; functional traits; food webs; rainforests.

INTRODUCTION

Whilst they only represent 6 to 7 % of continental surfaces, tropical rainforests shelter more than half of the Earth's species **(Wilson 1988)**. Epiphytes, non-parasitic plants (*e.g.*, ferns, orchids, bromeliads) that grow on other plants or trees, are conspicuous components of rainforest canopies and understories. These plants make a significant contribution to the structure and functioning of the forest’s biodiversity because, among other important ecological roles **(Nadkarni & Matelson 1989)**, they provide habitat and food resources to a more or less specialized fauna (*e.g.*, invertebrates, amphibians, reptiles), to the point that patches of epiphytes may contain more animal biomass than the surrounding tree crowns **(Ellwood & Foster 2004)**. Only a handful of studies have estimated the invertebrate biomass found in rainforest epiphytes **(Richardson *et al.* 2000b, Ellwood & Foster 2004, Petermann *et al.* 2015)**. Like abundance or density, biomass can be a proxy of the carrying capacity of any given habitat within its larger environment. However, these measurements are variable (seasonal changes can be significant) and represent snapshots in time **(Stork & Eggleton 1992)**. More importantly, these parameters tell us little about the turnover time of invertebrate populations, or about the relationships between community structure and ecosystem processes. Secondary production, the formation of heterotrophic biomass per unit surface area per unit time, is a measurement of the carbon and energy flow in ecosystems when estimated at the scale of a community **(Benke & Wallace 2014)**. Secondary production estimates encompass information on population density, growth rates and biomass turnover times, and, therefore, constitute an accurate way of quantifying (i) the proportion of species within food webs **(Benke *et al.* 1984)**, and (ii) the importance of specific habitat types in contributing animal biomass to their larger environment. Secondary production is influenced by food supply and temperature that modulate species’ growth rates. A species biomass turnover rate, or production:biomass (P:B) ratio (*i.e.*, the annual production divided by the mean annual biomass over the entire year), is negatively correlated with its lifespan and increases with the number of generations per year. The production statistics of coexisting species can therefore be used to question population to community level responses to the dynamics of their habitat template in relation to life history strategies (*e.g.*, small body size and fast life cycles *vs* larger, longer lived species) that allow the best use of the available food and habitat resources **(Pianka 1970)**. By and large, information on secondary production and animal population dynamics is of critical importance to any effort to predict ecosystem responses to environmental fluctuations, be they natural or anthropogenically driven. Despite their role as a keystone resource in tropical rainforests,, no previous study has ever estimated the secondary production sustained by any epiphyte, or, perhaps more importantly, the main drivers (including habitat features and species functional traits) behind the dynamics, annual production, and biomass turnover rates of epiphyte-associated invertebrate populations.

Bromeliads (Bromeliaceae) are flowering plants represented by 3,140 species native mainly to the Neotropics **(Givnish *et al.* 2011)**. The leaves of tank bromeliads are tightly interlocking, forming wells that collect rainwater and leaf litter. These small reservoirs hold a few milliliters to 45 liters of water and provide a habitat for aquatic organisms ranging from prokaryotes to macroinvertebrates **(Frank & Lounibos 2009, Brouard *et al.* 2012)** and occasionally vertebrates **(Poelman & Dicke 2008)**. In rainforests, tank bromeliads occur from the soil to the canopy and can reach a density of up to 175,000 individuals per hectare and impound up to 50,000 liters of water **(Sugden & Robins 1979, Richardson 1999)**. The incoming detritus (*e.g.*, leaf litter from overhanging trees, dead arthropods, feces) constitutes a source of nutrients for the aquatic food web and for the plant itself **(Benzing 2000, Leroy *et al.* 2015)**. Macroinvertebrates, mostly aquatic insect larvae, make up the dominant part of the animal biomass within tank bromeliads. Both observational studies and short-term experiments **(Richardson *et al.* 2000a, Ngai & Srivastava 2006)** showed that the bromeliad aquatic food web is tightly integrated into the structure and functioning (*i.e.*, leaf litter decomposition, nutrient retention, food resource for terrestrial predators, presence of emerging insects) of its broader rainforest environment. Because we lack an even basic understanding of how epiphyte-associated fauna contribute to energy flows within rainforest environments, the quantification of invertebrate production from the individual bromeliad to the level of a forest plot and its partitioning into invertebrate functional groups may help in estimating resource use in rainforests.

Secondary production and biomass turnover rates are thought to be influenced by the amount of food at the base of aquatic food webs, temperature, the stability of environmental conditions, and species richness and/or species identity **(Benke & Wallace 2014)**. Because the tank-bromeliad ecosystem is fueled by abundant leaf litter inputs in understorey environments **(Richardson *et al.* 2000b, Armbruster *et al.* 2002)** and because temperatures show little fluctuation in Neotropical forests (*e.g.*, this study), we hypothesized that fluctuations in environmental factors other than food and temperature influence the secondary production sustained by bromeliads by selecting invertebrate functional traits which allow some species to complete their life cycle in small, drought-sensitive systems. Specifically, we assumed that the most productive invertebrate species exhibit physiological, biological and ecological adaptations (*e.g.*, short life spans, dispersal abilities, respiration modes) that allow for *in situ* resistance in these systems.

Our study was conducted in French Guiana in a lowland rainforest typical of the Guyana Shield, the epicentre of bromeliad radiation and a hotspot for bromeliad faunal diversity. We studied the life cycles, growth rates and P:B ratios of the dominant species as well as the annual production of all of the aquatic invertebrates inhabiting a very common tank bromeliad species on the basis of samples taken at fortnightly intervals over one year. Annual production was estimated for individual invertebrate species, functional groups, the entire community of an average bromeliad, and a forest plot (here 5,000m²). We compare our secondary production estimates for communities with values available from the literature for other ecosystem types, and discuss how important tank bromeliads are in the formation of the heterotrophic biomass relative to their size (from the level of a plant to that of a forest plot). We then focus on the environmental factors (and species traits) that account for invertebrate population dynamics and production in these systems. Finally, we further elaborate on the importance of the presence in the surrounding rainforest of the insect biomass originating from the bromeliad through the emergence of adults.

MATERIAL AND METHODS

Study area and bromeliad species

French Guiana (FG) is an overseas region of France located on the north-eastern coast of South America. About 96% of its surface area (83,534 km^2) is covered by a remarkably species-rich equatorial forest **(Bongers *et al.* 2001)**. The Guianese primary forest remains one of the least impacted in the world, although gold mining and logging have strong localized impacts **(Dedieu *et al.* 2015)**. This study was in a lowland rainforest plot located near the

Petit-Saut Dam, Sinnamary (5°03’43’’N, 53°02’46’’W; elevation <80 m a.s.l.). The climate is tropical moist with 3,000 mm of annual precipitation, little seasonal variation in air temperature (monthly averages range from 20.5°C to 33.5°C), and a relative humidity oscillating between 70% and 100%. There is a major reduction in rainfall between September and November (Figure 1.1) and another shorter and more irregular dry period in March. *Vriesea splendens* (Brongn.) Lem. (Bromeliaceae, Tillandsioideae) is the only tank bromeliad in the understorey in the study area.

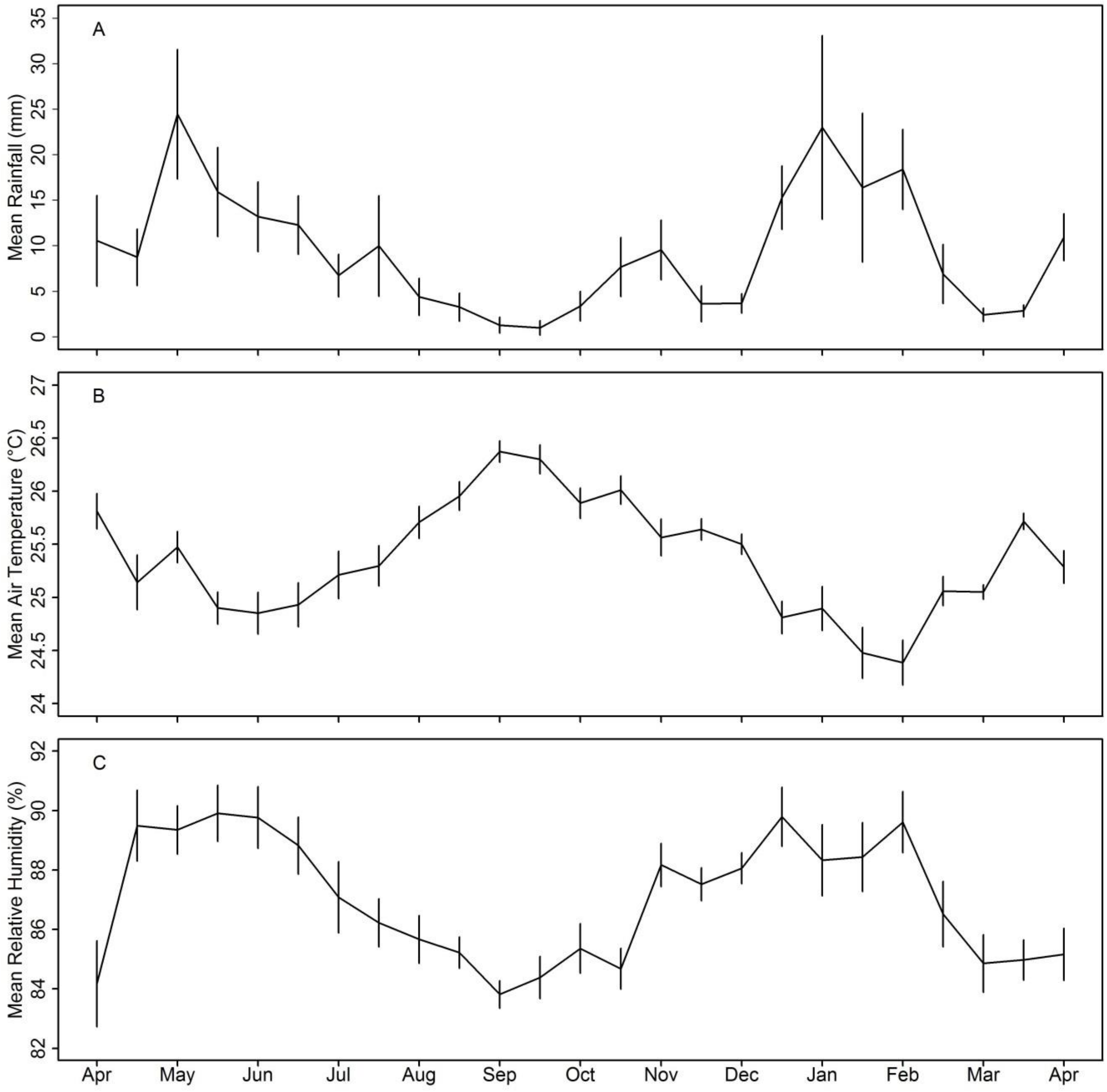

Figure 1.1 Weekly fluctuations in A) maximum precipitation (mm), B) air temperature (°C), and C) relative humidity (%) from April 2013 to April 2014. Bars represent standard errors.

Sampling procedure

A different group of three well-developed and undisturbed *V. splendens* (plant width= 0.5-1.0 m, excluding flowering individuals and juveniles) was sampled at fortnightly intervals from April 2013 to April 2014 for a total of 72 plants (N = 72). All of the plants selected were rooted on the soil or were epiphytes growing at <1m above the ground. We first extracted all of the coarse detritus fallen from overhanging trees (*e.g.*, leaf litter, twigs) from the rosette of each plant. The coarse detritus was rinsed in the field to collect the invertebrates. It was then dried at 60°C for 3 days and weighed to obtain a dry mass (DM, g). To sample the water and aquatic invertebrates in the plants, we used a 10-ml micropipette with the end trimmed to widen the orifice. The actual volume (V, ml) was measured using a 250-ml graduated cylinder for the first water extraction; the wells were then refilled with rainwater and sucked out again twice in order to maximize sampling efficiency. Although less efficient than plant dissection, we have already successfully used this non-destructive sampling technique **(Céréghino *et al.* 2011, Dézerald *et al.* 2015a)** as have others **(Jocqué *et al.* 2010)**. The sampled water was filtered through a 150µm mesh and the aquatic invertebrates were preserved in the field in 4% formalin (final concentration). Once a plant was emptied, we measured its maximum volume (Vm in ml) as the difference between a known volume of water used to fill the bromeliad and the remaining water volume in the graduated cylinder when the bromeliad overflowed. Finally, we recorded some key vegetative traits **(Céréghino *et al.* 2011)** to characterize the habitat structure of the aquatic invertebrates. The plant width (PW, cm) was measured as the maximum distance between the tips of the leaves (*i.e.*, an average of two 90° measurements); the average leaf width (LW, cm) was measured for five intermediate leaves and the total number of green leaves (NL) was counted.

Life cycles, growth rates, and secondary production

Aquatic invertebrates were identified to species or morphospecies (hereafter, “species”), enumerated in the laboratory and preserved in 70% ethanol (Table 1). Actual water volumes (V) at the time of sampling were used to calculate densities expressed as number of individuals per ml. All larvae were divided into 0.1mm-interval size classes based on measurements of non-deformable body parts (NDBP): *i.e.*, head capsule width, head capsule length, or carapace length. Measurements were used to identify the larval instars, and to construct size-frequency plots for life cycle determinations in all of the species studied.

For each species, sets of 10-20 individuals from the different size classes were dried at 60°C for 48h and weighed. The mean individual dry weights of the larvae (DW, mg) were deduced from linear regressions between the natural log of the weight (LnW) and the NDBP. Mean individual dry weights for each sampling date were log-transformed to generate a series of linear regressions that represent the cohorts' growth patterns over time. A specific growth rate (k, % dry weight per day) was calculated for each cohort using the following equation:

$$\mathrm{k} = 100\,.\left(\frac{\log(\frac{\mathrm{DW}i1}{DWi0})}{\text{t1-t0}}\right)$$

where $\mathrm{DW}i_1$ and $\mathrm{DW}i_0$ are the mean individual dry weights of the i$^{\text{th}}$ cohort at t1 and t0. Kendall rank correlations were used to test relationships between estimated growth rates and the mean value and coefficient of variation (hereafter, "CV") of temperature, precipitation, humidity, and the actual-to-maximum water volume ratio (a proxy of bromeliad hydrology) over each cohort development time.

The size-frequency method **(Hynes & Coleman 1968, Hamilton 1969, Benke 1979)** was used to obtain estimates of the cohort production (Pc) and annual production (P, mg DW ml^{-1} year^{-1}) from life history, abundance and biomass data. As for most life history studies, the abundance of the first size classes was underestimated, certainly due to their small size and shorter longevity **(Benbow *et al.* 2003)**. Hence, the density of each NDBP size class was corrected from the logarithmic equation obtained from the abundance plot for the average cohort **(Perán *et al.* 1999)**:

$$\mathrm{N} = -\mathrm{b}\ .\ \ln(\mathrm{NDBP}) + \mathrm{a}$$

where "a" and "b" are constants. Cohort production (Pc) and annual production (P) were then calculated as:

$$Pc = i\,.\sum_{j=1}^{i}\left[(N_{\mathrm{j}} - N_{\mathrm{j+1}})\,.\frac{1}{2}.(DW_{\mathrm{j}} + DW_{\mathrm{j+1}})\right]$$

and

$$\mathrm{P} = Pc\,.\left(\frac{365}{\mathrm{CPI}}\right)$$

where *i* is the number of size classes, N*j* is the mean number of individuals in a size class (*j*) during the year, Wj is the mean individual dry weight of a size class (*j*), and CPI is the cohort production interval (*i.e.*, number of days from hatching to the final size class). CPIs were estimated by a visual inspection of the size-frequency plots, and an average CPI was calculated from the CPIs of the various cohorts for each taxon. We also raised larvae in 50 ml tubes placed at ambient temperature to further refine the CPI estimates. A bootstrap procedure was used to account for variability in our production estimates **(Babler *et al.* 2008)**. We generated bootstrap replicates of production-to-biomass ratio estimates by randomly reassembling 1,000 data sets with replacement from the original data set collected for each plant by sampling date. Because the community structure can potentially change over time, we constrained the bootstrapped procedure to randomly sample data by sampling date. Subsequently, the median, first and third quartile from the 1,000 bootstrapped production-to-biomass ratios were presented for each species.

The size-frequency method yielded negative production values for *Corethrella* sp. and *E. bromeliarum*, even after correcting for the number of individuals within size classes. Such a case happens when no biomass loss occurs between successive size classes **(Stead *et al.* 2005, Babler *et al.* 2008)**. Based on the CPIs and annual biomasses (B), we calculated the production of these species (P) using the equation P = (365*B) / CPI. Although the cohorts obviously overlapped here, we were able to obtain reliable estimates of the CPIs for *E. bromeliarum* (70 days) and *Corethrella* sp. (10 days) by rearing individuals in tubes at ambient temperature.

Natural log-transformed total annual production estimates (mg DW ml^{-1} yr^{-1}) were regressed against the natural log-transformed total annual biomasses (mg DW ml^{-1}) for those species for which we described the life cycles and estimated the production using the size-frequency method. The resulting linear model was used to calculate the annual production of the remaining species (*i.e.*, rare species whose life cycles could not be described, 11 morphospecies and <8% of the total biomass) from their biomass estimates. In order to further assess the reliability of our estimates, we also calculated the secondary production of all species using Plante and Downing's model (1989); *i.e.*, log10(P) = 0.06 + 0.79 * log10(B) – 0.16 * log10(max individual mass) + 0.05 * (mean annual water temperature). All statistical analyses and figures in this study were generated using the R software version 3.1.2 **(R Core Team 2015)** and evaluated using a 95% confidence level.

Macroinvertebrate functional traits

In order to explore relationships between production-related statistics and the functional traits of invertebrates, we performed a mixed Principal Component Analysis (mPCA) on the 11 dominant species and their functional traits. The specific growth rate (k), mean cohort production interval (CPI), mean annual biomass (B), annual production (P), biomass turnover (P:B), and body size (BS) formed a first set of continuous variables that were rank-transformed. Locomotion (swimmers or crawlers; hereafter, "Loco1" or "Loco2"), respiration (tegument/gills or plastron/respiratory siphon; Resp1 or Resp2), body armor (soft bodied or sclerotized/shell; Boar1 or Boar2), and feeding habits (detritivore or predator; Feed1 or Feed2) were categorical variables with two levels each. The mPCA was conducted using the R-package *ade4*. All statistical analyses and figures in this study were generated using the R software version 3.1.2 **(R Core Team 2015)** and evaluated using a 95% confidence level.

Broadening the scale: from individual bromeliads to forest plots

Secondary production estimates for each species were used to estimate the annual production of the invertebrate community found in a medium-sized *V. splendens* bromeliad holding 100 ± 3.2 ml of water on average (± SE; n = 30). Therefore, the annual production of species per ml were added together and multiplied by 100. Production estimates were also separated into invertebrate functional feeding groups (FFGs *sensu* **Merritt & Cummins 1996**). The FFGs were based on the analyses of the gut contents of all of the species **(Dézerald *et al.* 2013)**. The estimate of the secondary production of an individual *V. splendens* bromeliad was applied to the surface area of the submerged part of its leaves, and then extrapolated to a square meter of bromeliad surface (*e.g.*, secondary production estimates expressed in g DW m^{-2} y^{-1}, as in the vast majority of studies of lakes, ponds and streams). Assuming that the submerged part of a reservoir is an inverted cone, we calculated the surface area using the mean reservoir height and radius (5.39 ± 0.3 and 1.9 ± 0.1 cm, respectively), and multiplied this value by the mean number of leaves forming wells (11.48 ± 0.34 wells; ± SE, n = 30) to obtain the total submerged surface area of the tank bromeliad.

The *V. splendens* were unevenly distributed in the forest. To estimate their density, we first delineated three 50 x 100 m plots that were far from each other. Then, within a given plot, we delineated four 10 x 10 m quadrats evenly distributed along a 100 m-long transect located in the middle of each plot. The bromeliad density was estimated by counting the number of plants within each quadrat. Their elevation above ground was measured using a laser distance meter (Leica DISTO™ D5). The maximum elevation in the supporting trees was 11.5 m, so we were confident that most if not all *V. splendens* were visible and could be counted. All of the bromeliads were divided into four size classes based on plant width (PW): "juveniles" (*i.e.*, tankless individuals), "small", "medium", and "large" plants. The maximum water volume of 30 plants from each size class was estimated using the same procedure as for the measurements of maximum volume (see above). Small, medium and large plants held on average 30.39 ± 2.10, 100.12 ± 3.20, and 234.21 ± 10.10 ml (mean ± SE) of water, respectively. The total amount of water held in plants at the scale of a forest plot was obtained by multiplying the average volume of each size class by the total number of plants within the same size class. As we found that all aquatic species can be found in all size classes (except *E. bromeliarum* and *Aulophorus superterrenus* that were absent from the "small" bromeliads), a production estimate was then extrapolated to the scale of a forest plot by multiplying the total amount of water held in the plants based on our estimate of the total annual production (P in mg DW ml^{-1} yr^{-1}). In the absence of secondary production estimates for epiphytes in rainforests, we compared our results to a literature review of production estimates for the dominant species in the community and at the community level in freshwater systems.

RESULTS

The population dynamics of dominant species

Overall, the apparent seasonal stability in macroinvertebrate density and biomass (Figure 1.2) resulted from the sum of population-specific abundance patterns. Several species showed seasonal patterns in density and biomass with a marked increase during the dry season, namely *W.* (*Dodecamyia*) *aphobema*, Ceratopogonidae sp.1, Orthocladiinae sp. and, to a lesser extent, *A. neivai* (Figure 1.3-1.5). Conversely, a few species did not show clear seasonal fluctuations in density and biomass (*e.g.*, *Corethrella* sp., *Cyphon* sp., and *Trentepohlia* sp.; Figure 1.3 and 1.4). All of the 11 dominant species (among 22, Table 1.1) were present in the system throughout the year. Their life cycles could be divided into two main groups based on the number of generations per year and the development time from hatching to last instar individuals. For all of the dominant species studied, the growth patterns (mean individual dry weight *vs* time) deduced from our interpretations of size-frequency plots showed repeated patterns over the year (Figure 1.6-1.11), suggesting that our identifications of cohorts and CPI estimates were satisfactory.

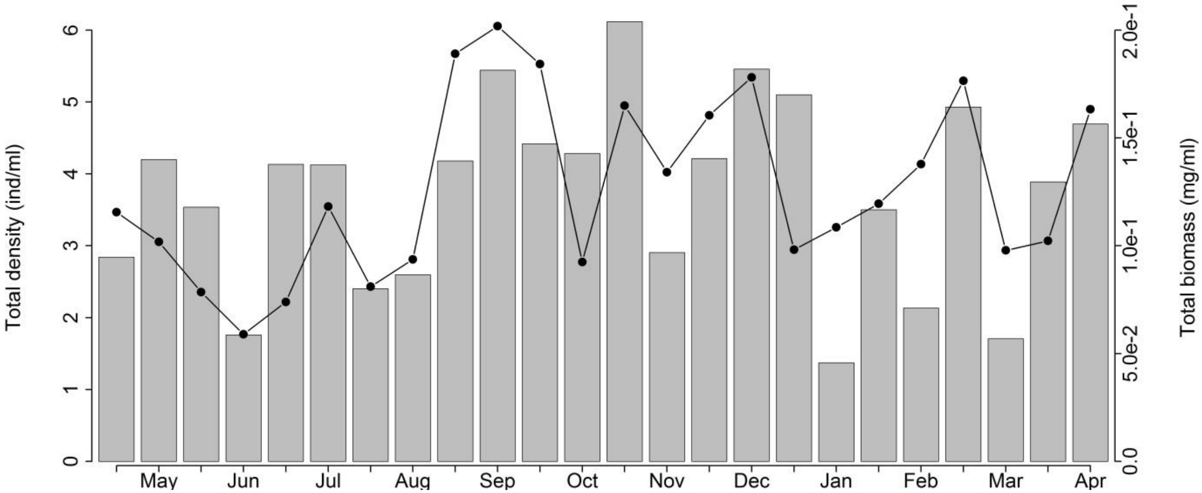

Figure 1.2 Recorded densities (ind ml^{-1}) and biomasses (bars and dotted lines, respectively; mg ml^{-1}) for all species throughout the year and associated variations in biomass (mg ml^{-1}; solid line).

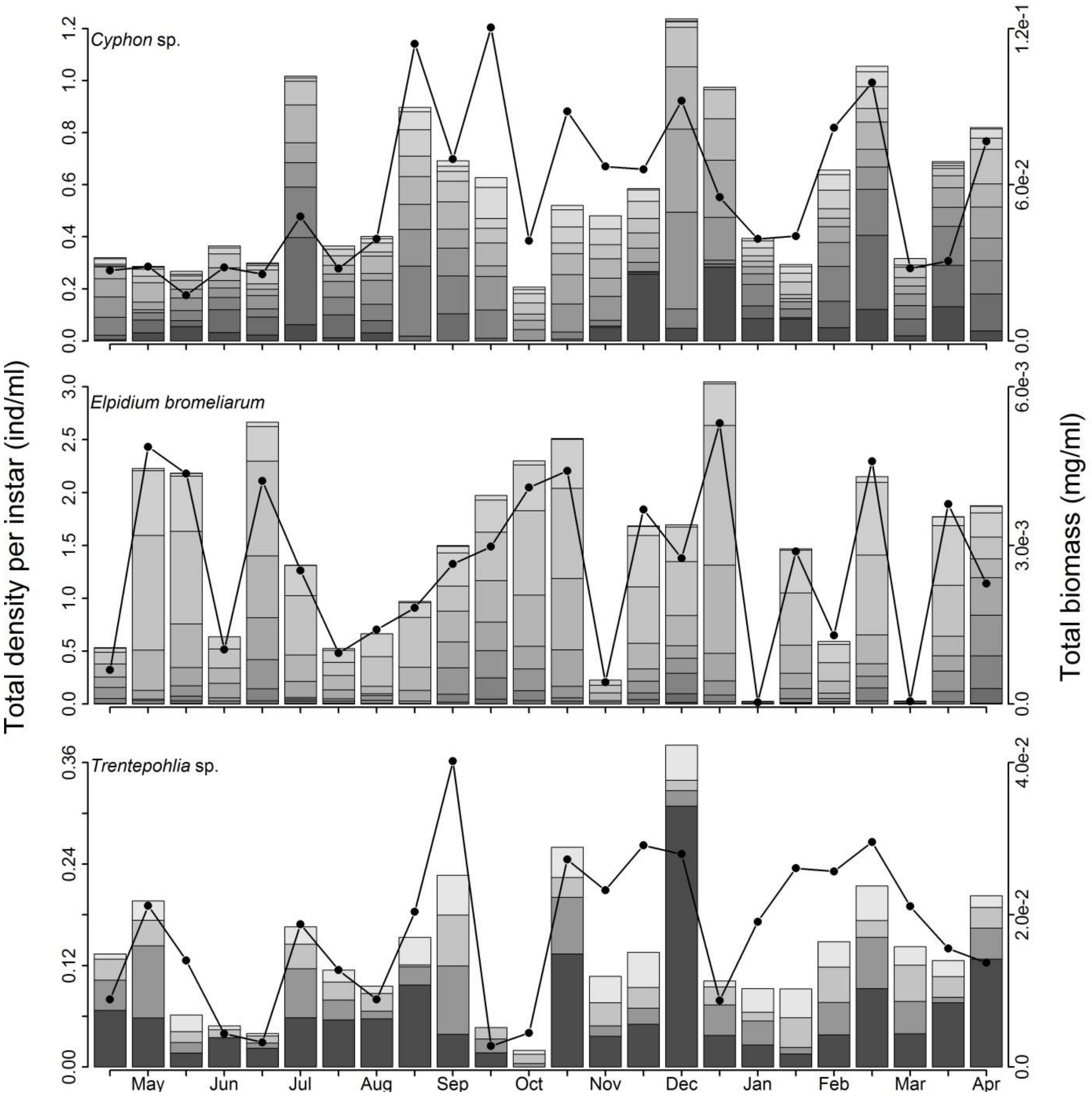

Figure 1.3 Recorded densities (ind ml-1) and biomasses (bars and dotted lines, respectively; mg ml-1) for Cyphon *sp.,* Elpidium bromeliarum*, and* Trentepohlia *sp. throughout the year (from April 2013 to April 2014). Shades of gray are for the various instars (first instar = bottom of the bar, last instar = top).*

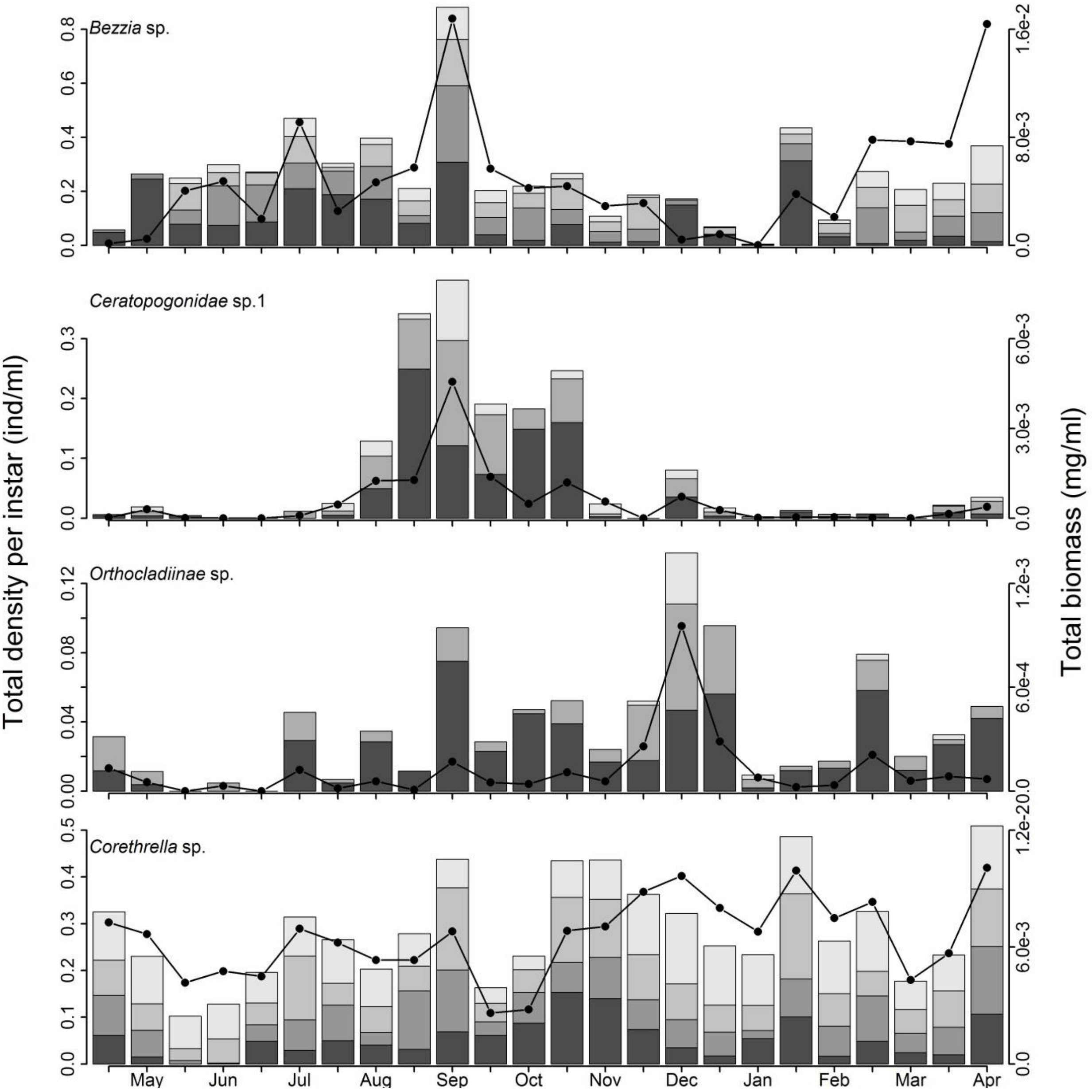

Figure 1.4 Recorded densities (ind ml-1) and biomasses (bars and dotted lines, respectively; mg ml-1) for Bezzia *sp., Ceratopogonidae sp.1, Orthocladiinae sp., and* Corethrella *sp. throughout the year (from April 2013 to April 2014). Shades of gray are for the various instars (first instar = bottom of the bar, last instar = top).*

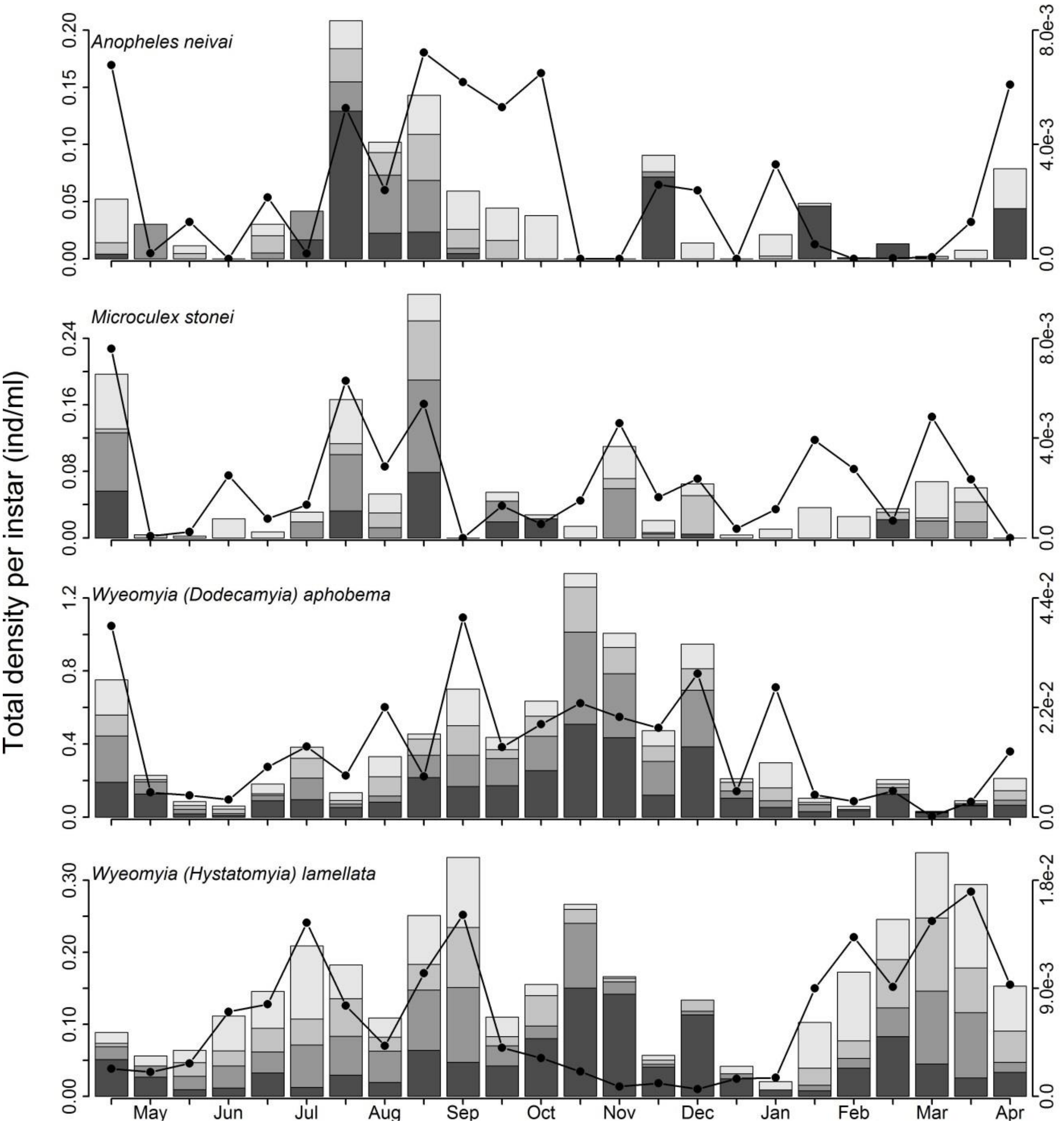

Figure 1.5 Recorded densities (ind ml-1) and biomasses (bars and dotted lines, respectively; mg ml-1) for Anopheles neivai, Microculex stonei, Wyeomyia (Dodecamyia) aphobema, *and* Wyeomyia (Hystatomyia) lamellata *throughout the year (from April 2013 to April 2014). Shades of gray are for the various instars (first instar = bottom of the bar, last instar = top).*

The first group included three species with (comparatively) longer larval lifespans (CPI= 1.5 to 3 months) and fewer than six generations per year; namely, *Cyphon* sp., *Trentepohlia* sp. and *E. bromeliarum* (Figure 1.6 and 1.9, and Table 1.1). The range in sizes was vast throughout the year, and individuals were present at all times. Despite the overlapping of generations, we were able to identify cohorts and development patterns. Hatching occurred throughout the year, except in October for *Trentepohlia* sp., and except during the dry season (mid-August to mid-December) for *Cyphon* sp. and *E. bromeliarum*.

During the rainy season (early May to August), the cohorts of *E. bromeliarum* were not distinguishable.

The second group included the remaining eight species. These fast growing species were all dipterans with three or four larval instars, a short larval lifespan (CPI= 10-30 days), and up to 22 generations per year. For the culicids *W.* (*Dodecamyia*) *aphobema* and *W.* (*Hystatomyia*) *lamellata*, instars were found throughout the year. The size-frequency and growth plots (Figure 1.7 and 1.8, and Figure 1.10 and 1.11) suggest that these species had 13 and 22 generations per year, respectively. The larvae grew quickly and emerged about 3 weeks after hatching all year round, so that there was no seasonal pattern of emergence. The culicids *A. neivai* and *M. stonei* had different development patterns where early instars (denoting hatching) were mostly present from July to September. Larvae grew from instar 1 to instar 4 within 1 to 1.5 months, but then seemed to remain at instar 4 over 1-2 months, so that these species presumably had *ca*. five generations per year. *Bezzia* sp. and *Corethrella* sp. also had four larval instars, and 13 and 15 generations per year, respectively, so that larval instars were present throughout the year. For *Corethrella* sp., pupae were also remarkably frequent. Orthocladiinae sp. and Ceratopogonidae sp.1 had three instars. The identifiable cohorts had a CPI of 20-27 days, suggesting the occurrence of 12-15 generations per year. We noted, however, that last instars of Orthocladiinae sp. were missing in our samples from April to November.

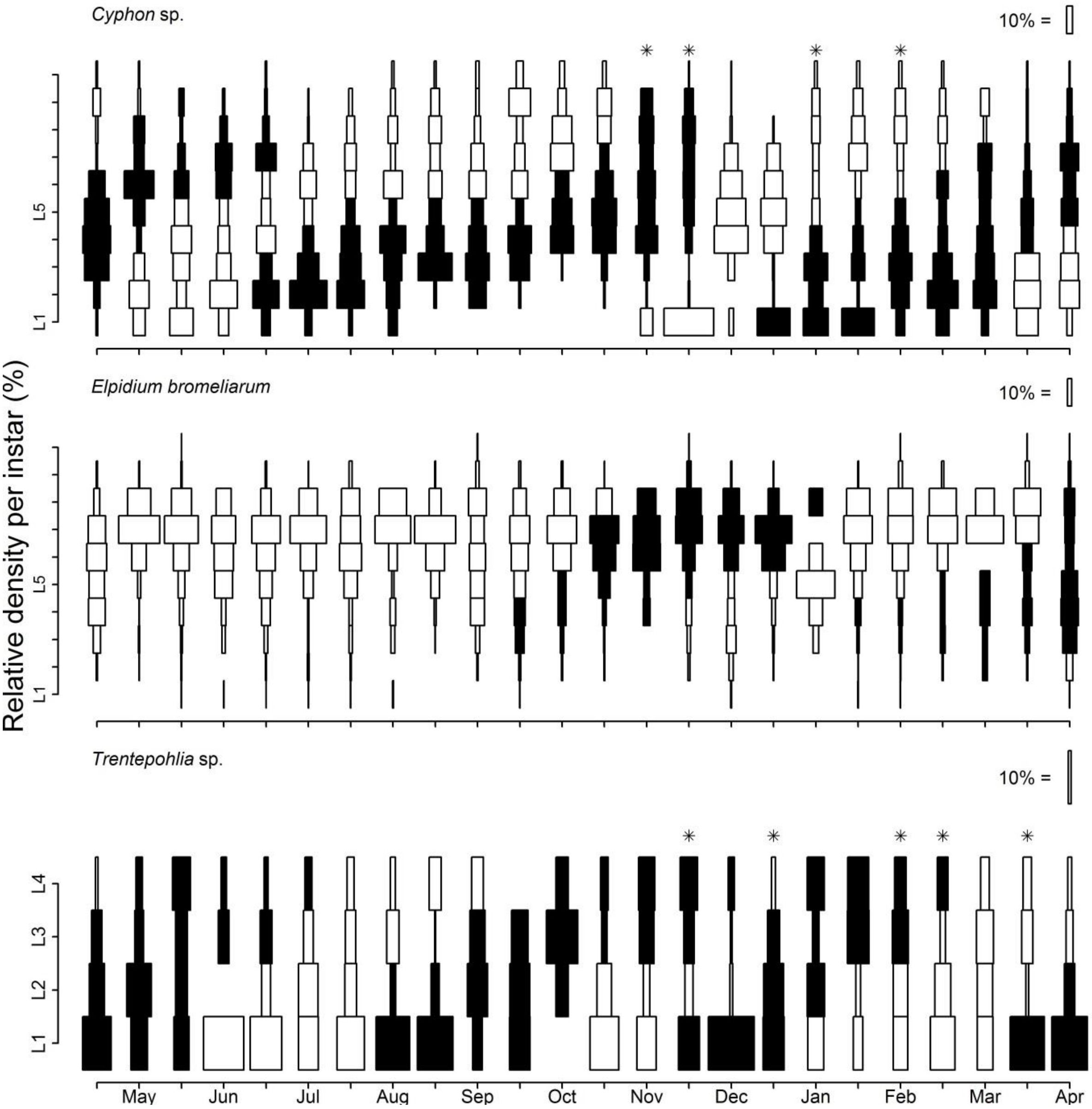

Figure 1.6 The life histories of Cyphon *sp.*, Elpidium bromeliarum, *and* Trentepohlia *sp. Frequency distribution of larval instars (L) deduced from the head capsule width for* Cyphon *sp. and* Trentepohlia *sp. and carapace length for* E. bromeliarum *by sampling date (from April 2013 to April 2014). The asterisks indicate periods of emergence.*

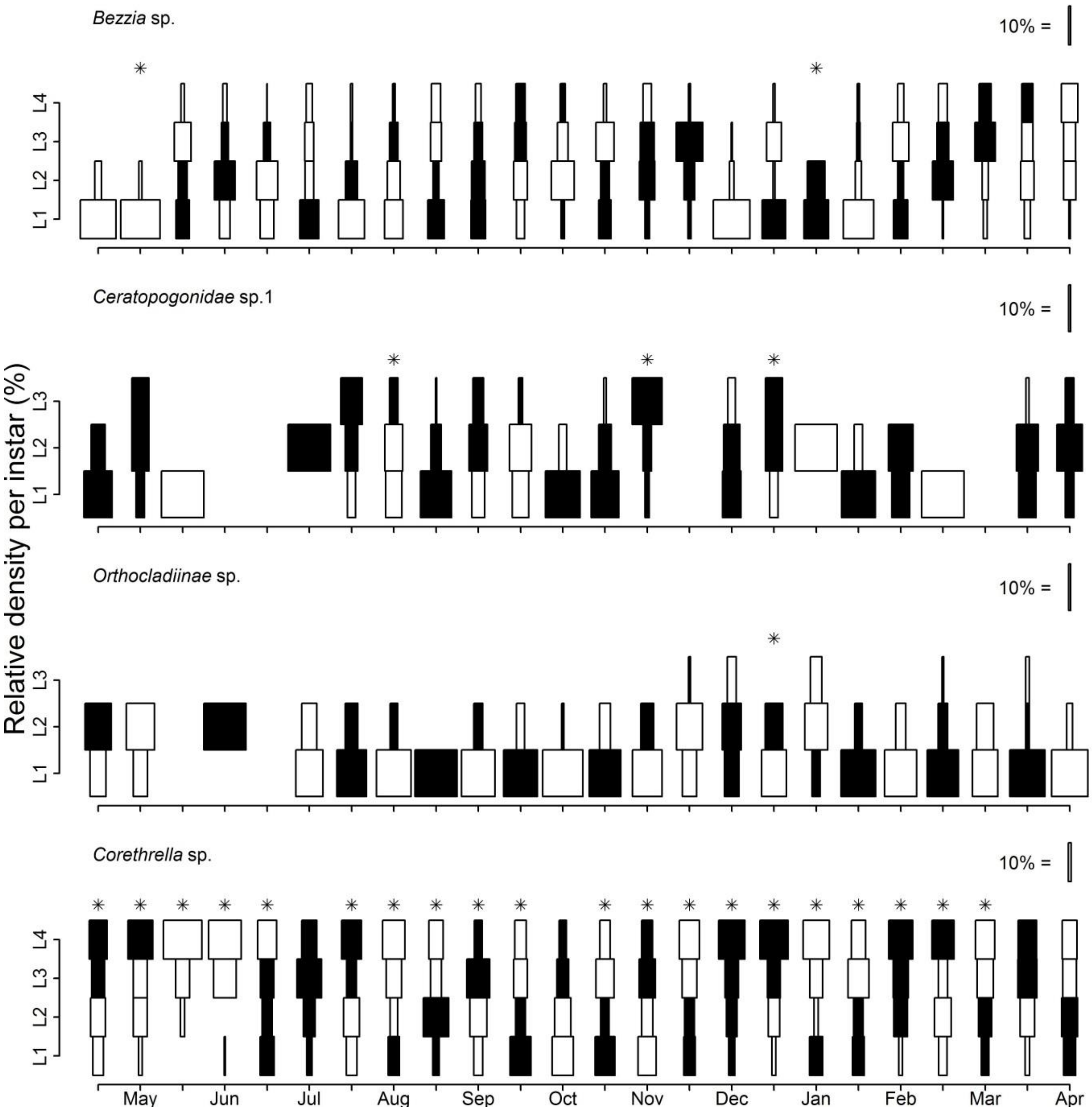

Figure 1.7 The life histories of Bezzia *sp., Ceratopogonidae sp.1, Orthocladiinae sp., and* Corethrella *sp. Frequency distribution of larval instars (L) deduced from the head capsule length for* Bezzia *sp. and width for Ceratopogonidae sp.1, Orthocladiinae sp., and* Corethrella *sp., by sampling date (from April 2013 to April 2014). The asterisks indicate periods of emergence.*

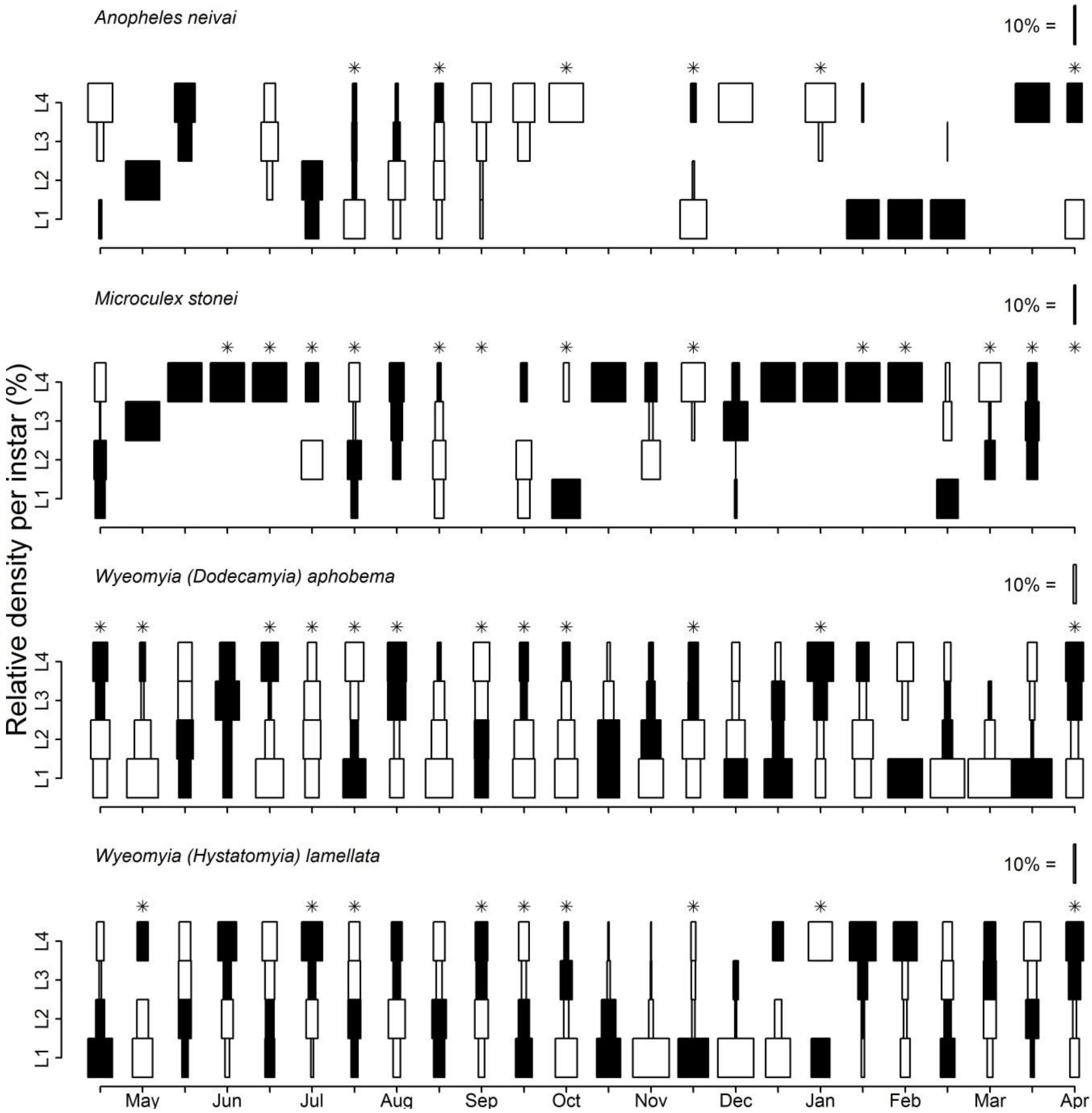

Figure 1.8 The life histories of Anopheles neivai*,* Microculex stonei*,* Wyeomyia (Dodecamyia) aphobema*, and* Wyeomyia (Hystatomyia) lamellata*. Frequency distribution of larval instars (L) deduced from the head capsule width by sampling date (from April 2013 to April 2014). The asterisks indicate periods of emergence.*

There was a significant linear relationship between the logarithm of the mean individual dry weight and the development time of each cohort for each species. On average, growth rates (k) ranged from 10 to 20 % dry weight per day for fast growing species, whereas they were between 3 and 7 % dry weight per day for *Cyphon* sp., *E. bromeliarum*, and *Trentepohlia* sp. (Figure 1.9, Table 1.1). We noted that *Cyphon* sp. and *Trentepohlia* sp. larvae that hatched during the dry season tended to grow faster than larvae that hatched during the rainy season (Figure 1.9). A total of 80 rank correlation tests were performed on the growth rates of the dominant species (save the culicid *M. stonei*; only two cohorts were identified) *vs* the mean and CV for temperature, precipitation, humidity, and actual-to-maximum volume ratio. The growth rates of *Corethrella* sp. and *Trentepohlia* sp. were negatively correlated with the CV of temperature (Kendall’s Tau = -0.48, *P* = 0.01 and Kendall’s Tau = -1, *P* = 0.02, respectively). The growth rates of *Corethrella* sp. were negatively correlated with the mean amount of precipitation and the CV of precipitation (Kendall’s Tau = -0.39, *P* = 0.04; Kendall’s Tau = -0.44, *P* = 0.04; respectively). Other relationships between species and variables were not significant.

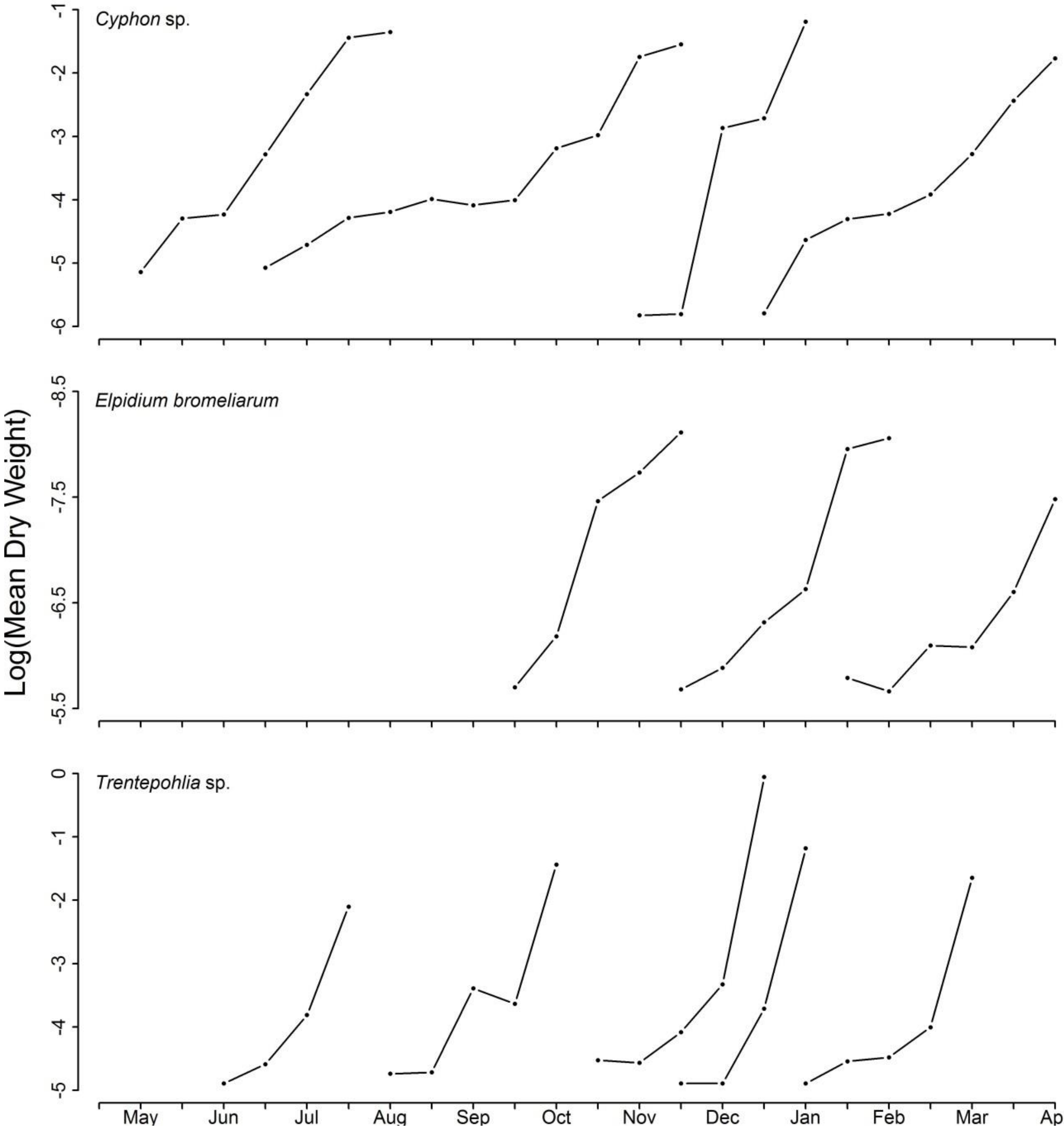

Figure 1.9 Mean individual dry weight (mg, natural log-transformed) as a function of time, depicting the growth patterns of identified cohorts of Cyphon *sp.,* Elpidium bromeliarum*, and* Trentepohlia *sp. (from April 2013 to April 2014).*

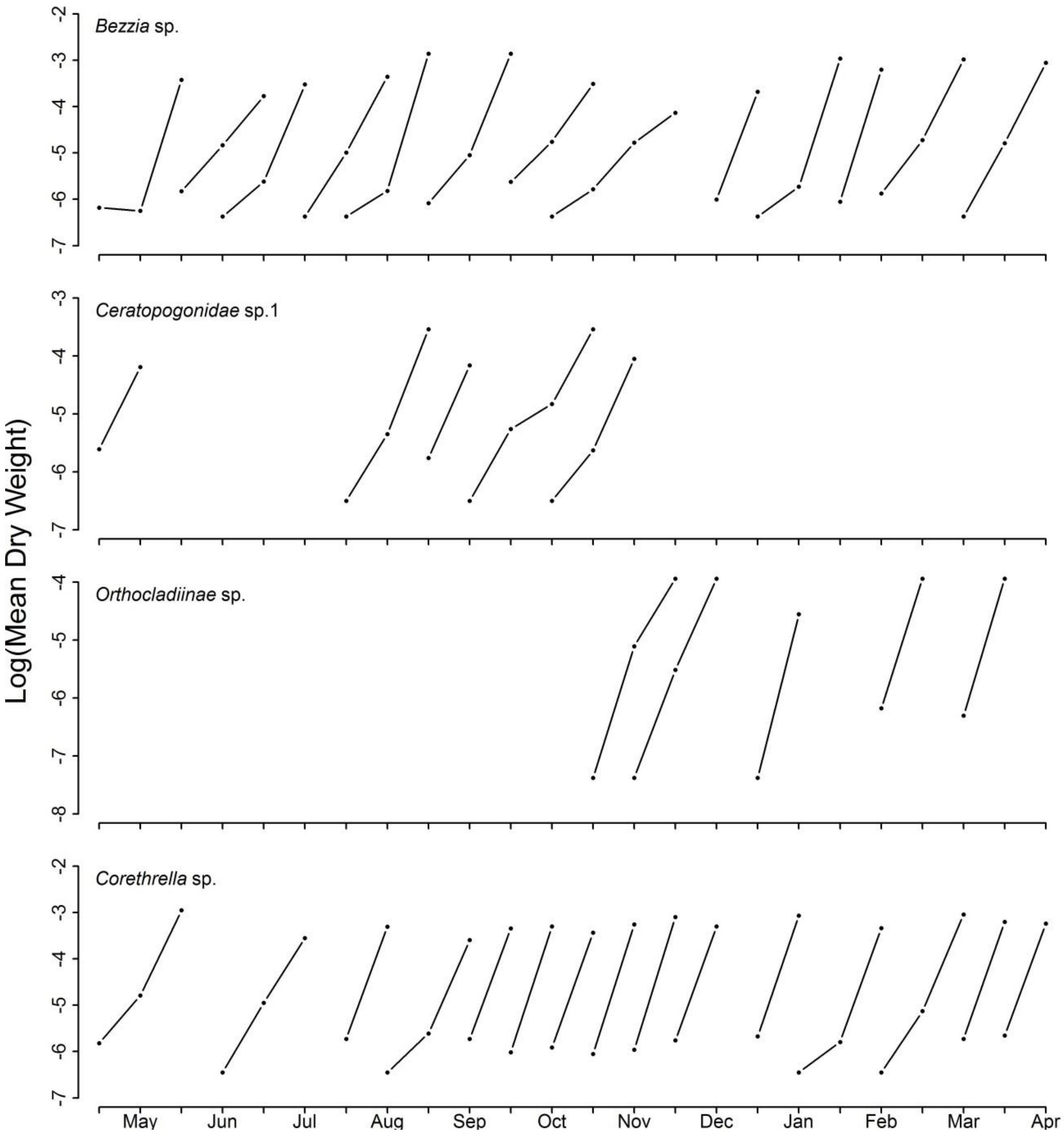

Figure 1.10 Mean individual dry weight (mg, natural log-transformed) as a function of time, depicting the growth patterns of identified cohorts of Bezzia *sp., Ceratopogonidae sp.1, Orthocladiinae sp., and* Corethrella *sp. (from April 2013 to April 2014).*

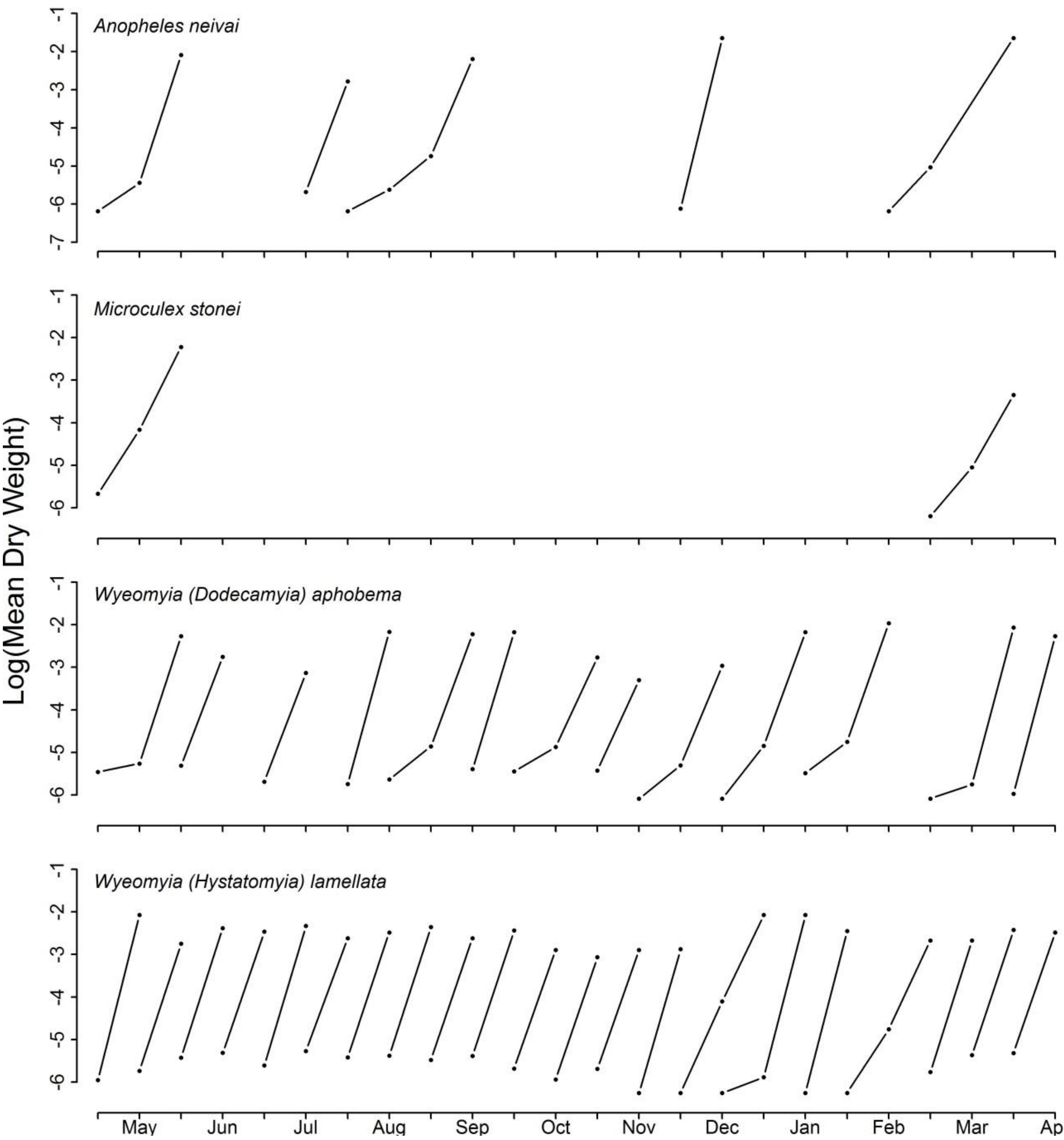

Figure 1.11 Mean individual dry weight (mg, natural log-transformed) as a function of time, depicting the growth patterns of identified cohorts of Anopheles neivai, Microculex stonei, Wyeomyia (Dodecamyia) aphobema, Wyeomyia (Hystatomyia) lamellata *(from April 2013 to April 2014).*

Secondary production of species

The production estimates of the dominant species were calculated using the size-frequency method (except for *Corethrella* sp. and *E. bromeliarum*, see Material and Methods). For other species (rare species, life cycles not described), we used a regression analysis to infer production estimates (Figure 1.12). The species pool of the community was represented by a total of 22 morphospecies. The 11 dominant ones represented 92.3% of the mean annual biomass of the system. For the remaining species (7.7%), 5.6% of the biomass corresponded to *A. superterrenus* (Oligochaeta) and *Brachycera* spp.

Our production estimates for all species are provided in Table 1.1. In rank order, the most productive species were the coleopteran *Cyphon* sp. (0.42 mg DW ml^{-1} $year^{-1}$) and the dipterans *W.* (*Dodecamyia*) *aphobema* (0.3 mg DW ml^{-1} $year^{-1}$), *Corethrella* sp. (0.28 mg DW ml^{-1} $year^{-1}$) and *Trentepohlia* sp. (0.2 mg DW ml^{-1} $year^{-1}$). With its long generation times and low individual weights, the ostracod *E. bromeliarum* exhibited an intermediate rate of secondary production (0.015 mg DW ml^{-1} $year^{-1}$), although it was the most abundant species (1.4 individuals per milliliter on average). *Cyphon* sp. and *E. bromeliarum* had among the lowest turnover ratios (P:B = 5.8 and 5.2, respectively). The P:B ratio calculated for other species mostly ranged between 10 and 42 (Table 1.1). Overall, the medians of 1,000 bootstrapped P:B ratios confirmed the P:B estimates obtained through the size-frequency method (Table 1.1). However, considering the surprisingly low P:B estimate and life history patterns for the culicid *M. stonei*, it is likely that the bootstrapped P:B ratios provided more reliable values than the odd P:B values initially calculated for this species (2.2 to 9.95).

The linear regression between the natural log-transformed annual production and the mean annual biomass of the dominant species (except *Corethrella* sp. and *E. bromeliarum*) was highly significant ($R^2 = 0.74$, $P = 0.003$; Figure 1.12). The regression equation was log10(P) = 0.809 * log10(mean annual B) + 0.595. This equation was used to estimate the production of rare species based on their mean annual biomass, and we also provide calculations for all species according to the method developed by Plante and Downing (1989) (Table 1.1). Overall, the two methods differed in their estimations of annual production for individual taxa by an average factor of 11.03 ± 2.4 (±SE, n = 22; range from 2.06 to 72.65). This factor dropped to 7.4 ± 0.6 when *M. stonei* and *E. bromeliarum* were excluded (±SE, n = 21; range from 2.06 to 10.81). Community-level estimates using different methods differed by a factor of 4.7.

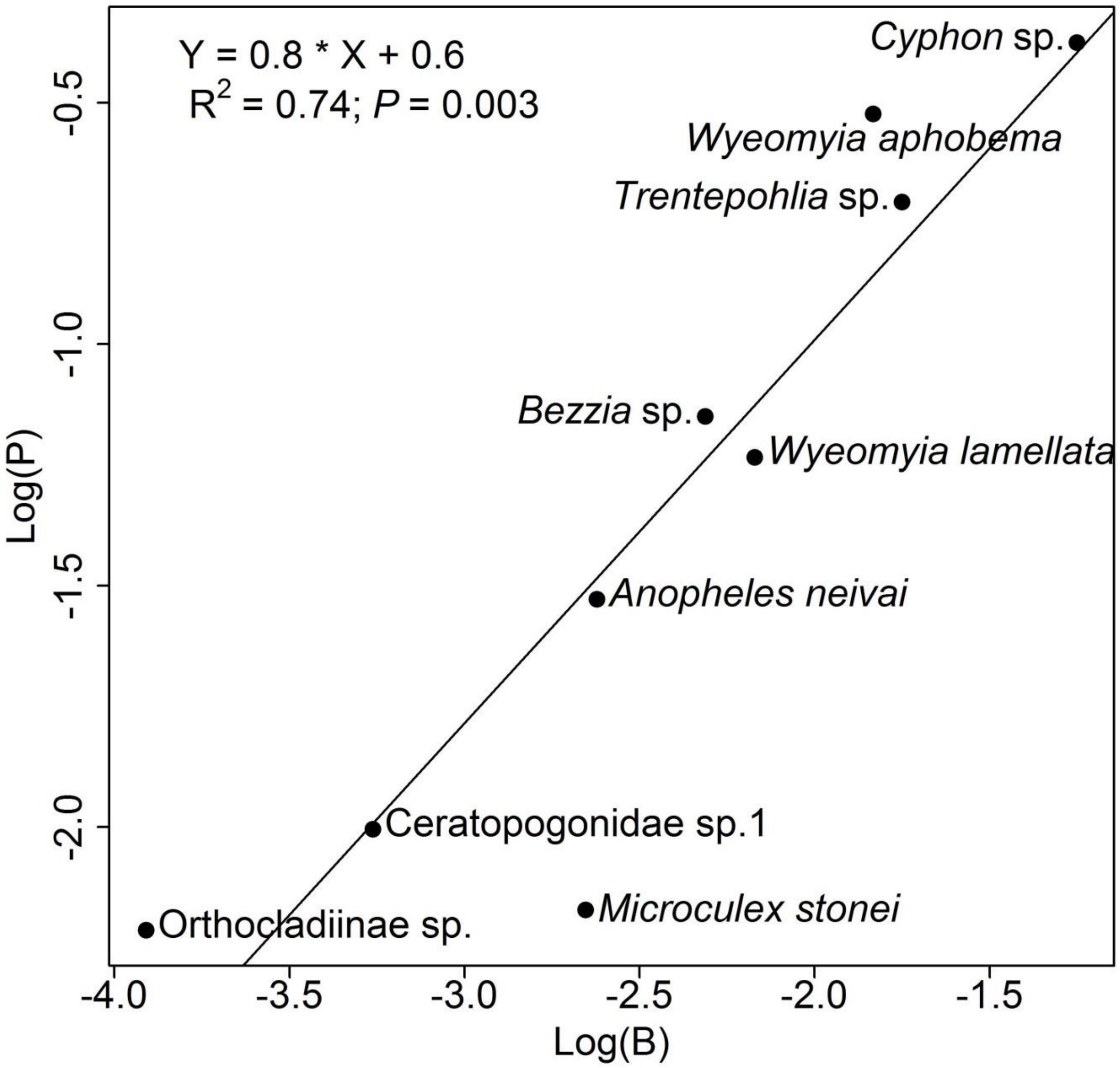

Figure 1.12 Natural log transformed production estimates (mg DM ml^{-1} year^{-1}) regressed against the natural log transformed biomasses (mg DM ml^{-1}) of nine species for which we determined the life history and estimated production using the size-frequency method.

Macroinvertebrate functional traits

The first three axes of the mPCA explained 35.7%, 23.9%, and 16.9% of the total variance in invertebrate traits, respectively. The first axis was negatively correlated with generation time (CPI), the presence of legs or pseudopods (Loco2) and of a sclerotized body or a shell (Boar2), and was positively correlated with growth (K), P:B ratio, ability to swim (Loco1) and a soft body (Boar1; Figure 1.13). In other words, species with legs or pseudopods that are able to move from leaf to leaf (*e.g.*, to find water during dry periods) and resist desiccation thanks to their exoskeleton (*e.g.*, *Cyphon* sp., *Trentepohlia* sp., *E. bromeliarum*) have longer generation times and slower individual growth than those soft-bodied species that swim in the water column (*e.g.*, culicids). The second axis was mainly defined by the mean annual production (prod) and biomass (biom) of species, suggesting that secondary production (axis 2) is constrained by a trade-off between rapid growth, high biomass turnover and short generation time (axis 1). Finally, the third axis was characterized by the respiration mode, feeding habits, and, to a lesser extent, body size (Figure 1.13).

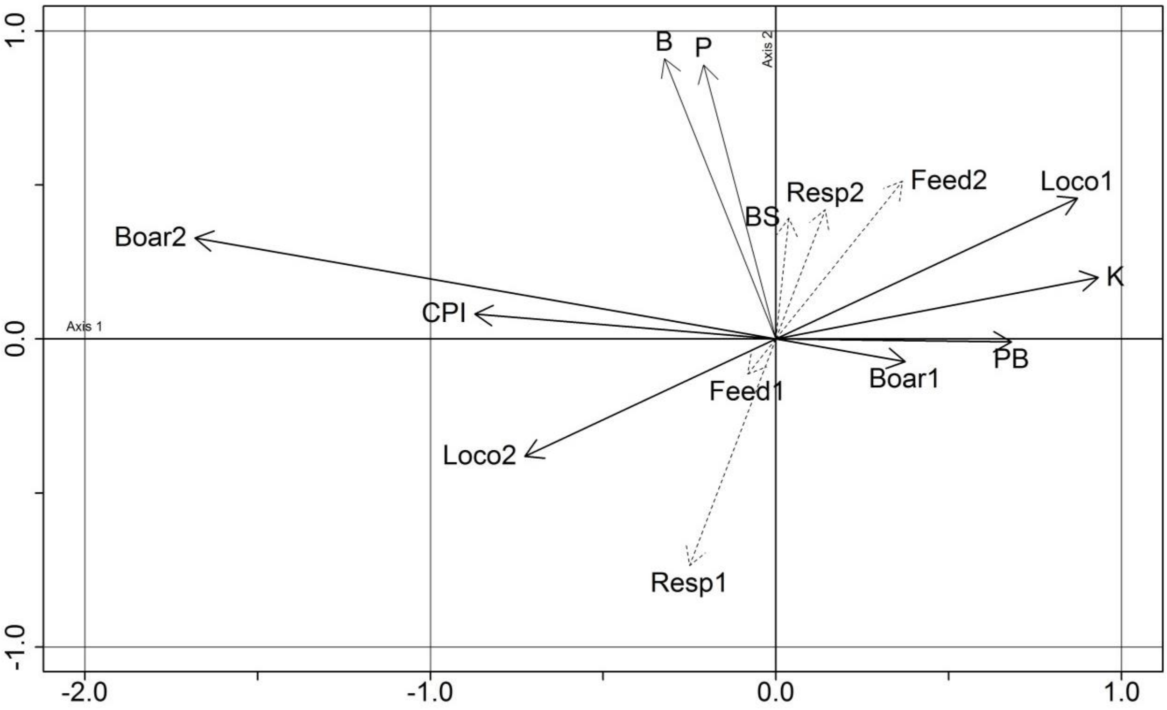

Figure 1.13 Mixed Principal Component Analysis biplot showing correlations among functional traits. Arrow directions show the gradients and correlations among variables, arrow length represents the strengths of the variables on the ordination space. K = growth rate, CPI = cohort production interval, B = mean annual biomass, P = mean annual production, PB = biomass turnover (units as in Table 1.1), BS = body size, locomotion (swimmers or crawlers; Loco1 and Loco2), respiration (tegument/gills or plastron/syphon; Resp1 and Resp2), body armor (soft bodied or sclerotized/shell; Boar1 and Boar2), and feeding habits (detritivore or predator; Feed1 and Feed2).

Broadening the scale: from individual bromeliads to forest plots

Based on our results, a single medium-sized *V. splendens*, holding 100 ml of water on average, produced 150 mg DW of invertebrates per year. After converting this estimate to the surface area of the tank bromeliad, we obtain 8.96 g DW m^{-2} y^{-1}, a value that compares to the median values of 5.13 and 14.78 g DW m^{-2} y^{-1} for lakes and streams, respectively (data mainly derived from studies conducted in South, Central and North America, and tropical and subtropical Asia, and, to a lesser extent, Europe; see Table 1.2). Overall, the annual production of amphibiotic organisms (insects having an aquatic larval stage and a terrestrial adult) represented 93% of the total production in the system. Among this group, the Diptera and Coleoptera accounted for 70% and 30% of the production, respectively. Within the bromeliad food web, predators accounted for 24% of the annual production. The dominant predator in terms of production was *Corethrella* sp. Other predatory species were *Bezzia* sp., *Toxorhynchites haemorrhoidalis*, Tanypodinae sp., *Paravelia* sp., and an unidentified Coenagrionidae odonate. Although odonates are often seen as the typical top-predator in bromeliad ecosystems **(Petermann *et al.* 2015)**, damselflies (Coenagrionidae) are rare in the closed forests of French Guiana **(Brouard *et al.* 2012)** and their annual production was among the lowest in our system (0.0012 mg DW ml^{-1} yr^{-1}). Scrapers (*Cyphon* sp. and *E. bromeliarum*) and filter feeders (culicids) accounted for 29% and 26% of the annual production, respectively. Shredders (*Trentepohlia* sp.) and collector-gatherers (remaining species, Table 1.1) represented about 13% and 8% of the annual production, respectively.

We estimated that a 5,000 m^2 forest plot (a typical *V. splendens* patch size in the area) hosted 2,758 *V. splendens* (among which 979 were tankless juveniles) impounding 177 liters of water. This represents 1,779 tank bromeliads producing approximately 266.2 g DW of invertebrates per year (assuming no bromeliad mortality and a non-significant growth rate of the bromeliad population over one year). Overall, more than 90% of this production is exported to the surrounding terrestrial environment through the emergence of amphibiotic insects that leave the plants as adults.

Table 1.1 Annual production estimates of aquatic invertebrates in the tank bromeliad Vriesea splendens. *N= mean annual density ± SE (ind* ml^{-1}*); B= mean annual biomass ± SE (mg* ml^{-1}*), CPI= cohort production interval (days), SF-P and SF-P/B = annual production (mg* ml^{-1} $year^{-1}$*) and production-to-biomass ratios obtained using the size-frequency method, Boot-P/B and 1st-3rd Q = bootstrapped median of production-to-biomass ratio estimated using the SF method as well as the first and third quartiles (± SE); P&D-P and P&D-P:B = annual production (mg* ml^{-1} $year^{-1}$*) and production-to-biomass ratio estimates obtained using* **Plante and Downing***'s regressions* **(1989)**.

Taxa	N	B	CPI	SF-P	SF-P/B	Boot-P/B	1st-3rd Q	K	P&D-P	P&D-P/B
Diptera										
Culicidae										
Wyeomyia (*Dod*) *aphobema*	3.9e-1±7.1e-2	1.5e-2±2.4e-3	22.5±2.1	3.0e-1	33.2	32.50	28.4-38.4	15.2±1.5	9.0e-1	61.3
Wyeomyia (Hys) lamellata	1.6e-1±9.1e-2	6.7e-3±1.1e-3	17.0±1.1	5.8e-2	15.5	17.77	14.8-21.6	19.1±0.7	5.1e-1	76.8
Wyeomyia (Wyo) robusta	3.3e-3±8.0e-4	1.3e-4±5.6e-5		2.8e-3 *	21.6 *				2.2e-2	169.7
Microculex stonei	5.4e-2±1.5e-2	2.2e-3±4.2e-4	13.5±2.5	3.0e-3	2.2	9.95	5.6-14.8	10.5±1.0	2.2e-1	99.2
Anopheles neivai	4.3e-2±1.0e-2	2.4e-3±5.2e-4	27.0±5.6	3.0e-2	80.2	69.80	32.5-151.7	17.4±3.5	2.1e-1	89.1
Toxorhynchites haemorrhoidalis	1.0e-3±6.0e-4	3.5e-4±3.5e-4		6.3e-3 *	18.0 *				4.0e-2	114.7
Corethrellidae										
Corethrella sp.	2.9e-1±2.3e-2	6.8e-3±4.4e-4	10.0±1.3	2.8e-1 †	36.5 †			14.8±0.9	5.7e-1	84.5
Ceratopogonidae										
Bezzia sp.	2.6e-1±3.6e-2	4.9e-3±9.0e-4	28.8±2.1	7.1e-2	13.6	14.83	13.8-16.1	10.3±1.0	4.1e-1	84.7
Ceratopogonidae sp.1	7.3e-2±2.3e-2	5.5e-4±2.0e-4	27.0±5.6	9.9e-3	16.4	15.82	14.2-17.8	8.9±0.7	9.0e-2	164.4
Ceratopogonidae sp.2	1.1e-3±4.6e-4	1.5e-5±1.0e-5		4.8e-4 *	32.9 *				5.1e-3	352.5
Ceratopogonidae sp.3	6.3e-4±2.3e-4	8.3e-6±5.3e-6		3.1e-4 *	36.6 *				3.3e-3	396.0
Chironomidae										
Orthocladinae sp.	3.8e-2±7.1e-3	1.2e-4±4.0e-5	21.0±3.7	6.1e-3	44.2	42.81	37.9-49.0	14.5±1.4	3.0e-2	239.7
Tanypodinae sp.	1.7e-3±4.2e-4	6.9e-5±2.9e-5		1.7e-3 *	24.5 *				1.6e-2	241.3
Tanytarsini sp.	7.6e-4±3.1e-4	6.1e-5±4.2e-5		1.5e-3 *	25.0 *				1.4e-2	221.5
Tipulidae										
Trentepohlia sp.	1.4e-1±1.7e-2	1.8e-2±2.0e-3	54±3.7	2.0e-1	11.3	11.78	10.3-13.5	6.6±0.6	8.1e-1	45.3
Psychodidae										
Telmatoscopus	8.4e-4±2.1e-4	6.7e-5±2.9e-5		1.6e-3 *	24.6 *				1.5e-2	217.3
Brachycera spp.	3.3e-2±2.4e-3	6.7e-4±8.4e-5		1.1e-2 *	15.9 *				1.1e-1	162.5

Odonata										
Coenagrionidae										
Coenagrionidae sp.	9.2e-4±2.5e-4	4.6e-5±2.2e-5		1.2e-3 *	26.4 *				1.1e-2	246.1
Coleoptera										
Scirtidae										
Cyphon sp.	5.7e-1±6.0e-2	5.6e-2±6.2e-3	99.0±14.7	4.2e-1	5.8	5.39	5.1-5.7	4.5±1.1	2.0e+0	35.2
Podocopida										
Limnocytheridae										
Elpidium bromeliarum	1.4±1.8e-1	2.6e-3±3.3e-4	70.0±5.0	1.5e-2 †	5.2 †			3.2±0.5	3.4e-1	128.6
Haplotaxida										
Naididae										
Aulophorus superterrenus	2.5e-1±2.0e-2	7.4e-3±1.0e-3		7.4e-2 *	10.0 *				7.0e-1	94.6
Hemiptera										
Veliidae										
Paravelia sp.	1.0e-3±2.0e-4	1.1e-3±3.8e-4		1.5e-2 *	14.5 *				8.6e-2	80.2

** Y = Log10(P) = 0.809*log10(B) + 0.595; † values are calculated backward, starting with the CPI (see Material and Methods); production estimates are the final output after correction for differential growth rates between successive size-classe*

DISCUSSION

In tropical forests, epiphytes can be seen as autogenic ecosystem engineers **(Jones *et al.* 1994)**, in that they form habitats for invertebrate species that otherwise would not be present **(Ellwood & Foster 2004)**. Our detailed results indicate that bromeliads (and likely epiphytes in general) produce significant amounts of invertebrate biomass, thus providing insights into the function of the "bromeliad ecosystem" and its links to the rainforest environment. Bromeliads containing small bodies of water can produce as much invertebrate biomass per surface area per unit time as streams and lakes, but their contribution to the larger forest food web will obviously depend on bromeliad density in the area. We further discuss our findings from the factors that influence invertebrate population dynamics *per se* in individual plants, to the contribution of entire bromeliads patches to secondary production in rainforests.

Invertebrate population dynamics in bromeliads

The metabolic rates of ectotherms are affected by temperature, which strongly governs all aspects of population dynamics **(Régnière *et al.* 2012)**. Although daily to monthly variations in temperatures in our study area of the Neotropics were too low to generate significant seasonal changes in invertebrate development patterns, the high temperatures throughout the year (20.5 to 33.5°C on average) certainly explain the higher growth rates of bromeliad invertebrates compared to those taxa living in temperate regions **(Huryn & Wallace 2000)**. Despite seasonal variations in precipitation (and to a much lesser extent temperature), most species showed repeated, almost identical growth patterns throughout the year, and all larval instars were usually present at all times. There was only a trend for faster growth during the dry season in *Cyphon* sp. and *Trentepohlia* sp. (see Results), but growth rates were not generally correlated with variations in air temperature and precipitation, and densities/biomasses showed little response to environmental conditions (except for a few species only).

Interestingly, tank bromeliads in general show some hydrological inertia towards changes in precipitation, depending on their structural complexity and on the study location **(Zotz & Thomas 1999)**. Owing to their architecture (number of wells that subdivide the water volume, leaf arrangement), tank bromeliads form complex water reservoirs with a large capacity to buffer changes in precipitation **(Brendonck *et al.* 2015, Trzcinski *et al.* under revision)**. For instance, cessation of rainfall does not immediately translate into significant changes in the amount and/or chemistry of bromeliad water: at our study site, most bromeliads held water throughout the year and never dried out completely **(Dézerald *et al.* 2015a)**.

The frequency at which tank bromeliads dry out is unknown. However, because drought is a predictable feature of these systems and invertebrates have acquired adaptive responses to cope with them, only extreme drought likely cause dramatic changes in invertebrate communities, and presumably in production **(Poff 1992, Brewin *et al.* 2000, Leung & Dudgeon 2011)**. The combinations of functional traits and production statistics revealed tradeoffs shared by phylogenetically distant species, here coleopterans, dipterans and ostracods (Figure 1.13). We know that some bromeliad-dwelling invertebrates, notably Scirtidae (*Cyphon* sp.), and Tipulidae (*Trentepohlia* sp.), are able to move from leaf to leaf to find water (personal observations), while odonates (Coenagrionidae) were observed to crawl on the aerial parts of bromeliads to find prey in other wells **(Amundrud & Srivastava 2015)**. These functional traits confer more ecological resistance/flexibility towards drought compared to physiological traits, in that they trigger immediate responses to unsuitable conditions (*e.g.*, avoidance, mitigation, short range migrations). As a consequence, these species can channel more energy into the formation of biomass over longer time periods (lower growth and biomass turnover rates). Conversely, species that are restricted to the epiphyte itself (here, to the water column) and have soft bodies (*e.g.*, culicids, *Corethrella* sp.) are more exposed to habitat contraction/stochasticity, and channel more energy into fast larval growth and short hatching to emergence time (higher growth and biomass turnover rates). In a recent study, we indeed found that the invertebrate assemblages at our study site was drought-resistant until the water volume in the bromeliads dropped by 90%, and this was unambiguously related to traits like small body size and physiological resistance to desiccation **(Dézerald *et al.* 2015a)**. A related issue for future research is therefore to identify which functional traits are the strongest biological determinants of population-level production, and to assess which environmental factors act as a selective force (in the ecological, not evolutionary sense) that increase the prevalence of certain traits at the expense of other traits within communities. In summary, secondary production in our tank bromeliads was sustained by an abundant food supply (detritus), and by high ambient temperatures with low seasonal fluctuations. In addition, the buffering capacities of the plant itself (notably in terms of water retention time; “physical buffering”), together with the functional traits of the aquatic community that confer *in situ* resistance to desiccation (“biological buffering”), confer some stability to the tank-bromeliad ecosystem **(Trzcinski *et al.* under revision)**. As a result, invertebrate populations with rapid turnover times and overlapping generations can develop throughout the year exporting much of the energy trapped within the decaying leaves. Although we did identify cohorts, the dynamics of the invertebrate community as a whole could be summarized as “everything is everywhere at all times”.

Some issues in our production estimates deserve particular attention. In *Corethrella* sp. and *E. bromeliarum*, the size-frequency method yielded negative production values. Firstly, the duration of the last instar can be longer compared to previous instars, because last instars often need to store more energy for pupation and the adult stage **(Tammaru & Esperk 2007)**. Secondly, we assume mortality to be weak for these two species, as *Corethrella* sp. is the main predator with no sign of cannibalism, and gut contents of predators previously showed us that *E. bromeliarum* with its calcified shell is rarely preyed on **(Dézerald *et al.* 2013)**. Altogether these processes could explain why individuals in late instars were more likely to be sampled. In culicids, larvae from different cohorts tended to accumulate within the last instar, indicating that late instars may experience slower growth rates (possibly after reaching a refuge size from predators; **Dmitriew 2011**). *M. stonei* yielded unexpected results with a low P/B ratio for a culicid species (4.9), but here we barely found first instars whereas late instars were found throughout the year. Despite intriguing results for some species, Plante & Downing’s regression model and our own regression based on the size-frequency method yielded community-level estimates that differed by a factor of 4.7 on average (range: from 1.8 to 3.0 in **Stockwell & Johannsson 1997**, and **Butkas *et al.* 2011**). Assuming however that a greater level of confidence is achieved when several techniques agree on the relative importance of various production estimates, we note that the size-frequency and Plante & Downing methods agreed on the rank order for the two most productive to the seven least productive taxa. Whilst we based our study on the methodological backgrounds provided by studies of large freshwater systems that differ in their physical attributes (*e.g.*, size, boundaries), we concede that a few adjustments in our estimations related to the study of bromeliad systems were needed for a viable and meaningful comparison with those systems (*e.g.*, see also the study in snag habitats by **Benke & Wallace 2014**). Regardless of absolute estimates, our study therefore allows for comparisons of secondary production estimates within- and between taxonomic groups, and between ecosystems.

Are small habitats less productive?

Our study suggests that secondary production is not directly related to the size of the system nor to species richness, because the tiny tank-bromeliad ecosystem that contains only a few invertebrate species compares to some of the much larger ecosystems in terms of heterotrophic biomass formed per unit area per unit time. Assuming that smaller systems contain less species (an individual bromeliad hosted up to 14 species) and that more productive sites host more species **(Srivastava & Lawton 1998)**, we *a priori* expected very small production estimates for bromeliads when compared to much larger ecosystems. Based on our literature review, secondary production ranges from 0.04 to 223.9 g DW m^{-2} y^{-1} (min-max) in lakes, and from 0.69 to 639.4 g DW m^{-2} y^{-1} in streams worldwide (Table 1.2). Bromeliads fall within the range of their median values (see results). It is worth noting that estimates for freshwaters in general are for systems that host >100 species **(Benke & Wallace 2014)**, among which many taxa are absent (*e.g.*, Bivalvia, Ephemeroptera), rare (*e.g.*, Dytiscidae), and/or less species-rich (*e.g.*, Chironomidae, Oligochaeta) in tank bromeliads. Therefore, even though high production estimates are sometimes associated with low taxonomic diversity **(Benke & Wallace 2014)**, the relationship between invertebrate diversity and secondary production would deserve to be further explored. Our study of small bromeliad ecosystems, that only host between 7 and 14 species per plant but sustain a high secondary production similar to larger ecosystems, suggests that species identity and habitat characteristics (including stability), rather than species richness and habitat size *per se*, mediate differences in secondary production among ecosystems.

The production of bottom-up facilitators is crucial in supporting the production of the whole invertebrate community (by transferring energy/nutrients to the upper-trophic level) in typical detritus-based systems. Food webs in tank bromeliads mainly rely on the decomposition of leaf litter from the surrounding tree canopy **(Benzing 2000)**. We found that scrapers dominated the system (29% of the annual production), followed by filter feeders (26%), predators (24%), shredders (13%), and collectors (8%). A recent review of production in small temperate streams **(Wallace & Eggert 2009)** highlighted a reverse pattern, where collectors, shredders, predators, filter feeders, and scrapers, represented on average 31%, 27%, 19%, 15%, and 8%, respectively, of the total secondary production. However, these patterns were quite variable among streams in various landscapes (prairies, deciduous forests). The generality of the pattern we found at our study site could thus be explored in bromeliads growing in sun-exposed areas **(Brouard *et al.* 2012)**. Shredders are theoretically responsible for the processing of coarse detritus, so their low contribution to the overall community production in bromeliads suggests that i) they are keystone species that have a disproportionate impact on decomposition rates relative to their abundance/production, and/or ii) invertebrates that scrape off the leaf surfaces play an overlooked role in reducing the coarse detritus to smaller particles, and/or iii) microbial activity plays a key role in supporting the overall invertebrate production through bottom-up facilitation **(LeCraw 2014)**.

Do bromeliads matter for secondary production?

Cross-ecosystems fluxes of individuals, energy and matter at ecotones play a major role in the functioning of both ecosystem types **(Baxter *et al.* 2005, Wallace *et al.* 2015)**, so it is likely that tank bromeliads make a significant contribution to the forest invertebrate food web as a whole. We estimated that a bromeliad patch can produce up to 266.2 g DW of invertebrates per year. A typical primary forest area of 5,000 m^2 in French Guiana is not densely populated by *V. splendens*. Our estimations yielded less than 6,000 individual plants per hectare while other studies counted from 25,000 to 175,000 bromeliads per hectare in Ecuador and Colombia **(Sugden & Robins 1979, Martinson *et al.* 2010)**. Also, although our study focused on the aquatic taxa present in tank bromeliads, terrestrial residents and visitors use these plants as a source of nutrients, permanent habitat, or as a moist refuge **(Gonçalves-Souza *et al.* 2010, Sabagh & Rocha 2014)**. Regardless of visitors, we therefore believe that our conservative estimates of the secondary production sustained by individual bromeliads to bromeliad patches would be much higher if terrestrial arthropods were considered too.

The production of the bromeliad biota is certainly profitable to the terrestrial biota; for instance, insect adults emerging from tank bromeliads are preyed on by spiders **(Romero & Srivastava 2010)**. Assuming that tank bromeliads throughout the Neotropics contain mostly aquatic insect larva and pupa **(Frank & Lounibos 2009)**, a conservative export estimate of 90% of the production in French Guiana, would have a substantial impact on the surrounding forest by attracting a wide variety of terrestrial taxa either seeking wet refuges or foraging at ecotones. This issue remains however unexplored, and could deserve further attention in the future – for instance by tracing the fate of isotopic C and N from the bromeliad-dwelling invertebrates to the terrestrial food web, while comparing the topology of arthropod food webs in areas with and without bromeliads. Whilst bromeliad food webs process abundant detrital inputs (leaf litter), they likely export most of their secondary production to the surrounding forest, production which would not exist if bromeliads were not present. Such a two-way interaction (processing of incoming detritus, exportation of insect biomass) may thus have a substantial impact on the whole ecosystem functioning in terms of the pathways represented in the energy budget.

Table 1.2 Literature review of published annual production estimates for invertebrate communities, adapted and updated from **Gratton and Vander Zanden (2009)**. *Production estimates that were originally provided either in g C* m^{-2} y^{-1} *or in g AFDW* m^{-2} y^{-1} *were converted to g DW* m^{-2} y^{-1} *using published conversion factors* **(Cummins & Wuycheck 1971, Strayer & Likens 1986, Gratton & Vander Zanden 2009)**.

Lakes, Ponds **Countries**	**Lake/pond names**	**g DW. $m^{-2}.y^{-1}$**	**References**
Texas, USA	Texas pond	10.76	**Benson *et al.* 1980**
Alaska, USA	tundra pond J	7.31	**Hobbie 1980**
Alaska, USA	tundra pond D	2.36	**Hobbie 1980**
Alaska, USA	tundra pond B	1.67	**Hobbie 1980**
Michigan, USA	Crampton Lake	4.6	**Babler *et al.* 2008**
Ontario, Canada	Batchawana Lake	0.11	**Dermott 1988**
Ontario, Canada	Wishart Lake	0.04	**Dermott 1988**
Ontario, Canada	Turkey Lake	0.27	**Dermott 1988**
Ontario, Canada	Little Turkey Lake	0.09	**Dermott 1988**
California, USA	Castle Lake	0.8	**Vander Zanden *et al.* 2006**
UK	Alderfen Broad	12.22	**Mason 1977**
UK	Upton Broad	13.11	**Mason 1977**
Manitoba, Canada	Lake Manitoba	17.38	**Tudorancea *et al.* 1979**
Ontario, Canada	Bay of Quinte	35.82	**Johnson & Brinkhurst 1971**
Canada-USA	Lake Ontario	16.16	**Johnson & Brinkhurst 1971**
UK	Eglwys Nunydd Res.	38.64	**Potter & Learner 1974**
UK	Loch Even	48.58	**Potter & Learner 1974**
Finland	Lake Paarjavi	5.13	**Sarvala *et al.* 1981**
Norway	Ovre Heimdalsvatn	2.62	**Larsson *et al.* 1978**
New Hampshire, USA	Mirror Lake	12.89	**Strayer & Likens 1986**
New York, USA	Findley Lake	1.56	**Wissmar & Wetzel 1978**
British Columbia, Canada	Marion Lake	7.56	**Wissmar & Wetzel 1978**
Wisconsin, USA	Lake Wingra	4.89	**Wissmar & Wetzel 1978**
Poland	Taltowisko	32.18	**Kajak & Rybak 1966**
Poland	Mikolajskie	16.69	**Kajak 1978** **Kajak & Rybak 1966**
Poland	Sniardwy	14.62	**Kajak & Rybak 1966**
France	Port-Biehl	2.18	**Laville 1975**
Northwest Territories, Canada	Char	0.56	**Welch 1973, Welch 1976**
Iceland	Lake Myvatn	43.8	**Jónasson *et al.* 1990**
Denmark	Hjarbaek Fjord	54.5	**Lindegaard & Maehl 1993**
Iceland	Thingvallavatn	3.98	**Jónasson *et al.* 1990**
Denmark	Esrom	34.47	**Jónasson *et al.* 1990**
Canada, USA	Erie	223.91	**Johannsson *et al.* 2000**
Germany	Brunnsee	6.89	**Bergtold & Traunspurger 2005**
Greenland	Lake 95	1.13	**Lindegaard & Maehl 1993**
Australia	Werowrap	71.53	**Patterson & Walker 1974**
USSR	Lake Zelenetzkoye	0.67	**Winberg *et al.* 1973**
USSR	Krivoe	0.62	**Alimov & Winberg 1972**

USSR	Krugloe	1.42	**Alimov & Winberg 1972**
USSR	Rybinsk Res.	3.56	**Sorokin 1979**
USSR	Dalnee L.	6.56	**Sorokin 1979**
USSR	Red	5.58	**Andronikova *et al.* 1972**
USSR	Naroch	3.56	**Winberg 1972**
USSR	Myastro	1.09	**Winberg 1972**
USSR	Batorin	3.53	**Winberg 1972**
USSR	Kiev Reservoir	46.6	**Gak *et al.* 1972**
USSR	Krasnoe	5.29	**Winberg 1972**
USSR	Drivyati	3	**Winberg 1972**
Canada, USA	Memphremagog	3.4	**Dermott *et al.* 1977**
Streams, creeks			
Countries	**Stream/creek names**	**g DW. $m^{-2}.y^{-1}$**	**References**
North Carolina, USA	CIII	14.62	**Benke 1993**
North Carolina, USA	CIV	12	**Benke 1993**
North Carolina, USA	CIV	4.6	**Benke 1993**
North Carolina, USA	CV	9.91	**Benke 1993**
Denmark	Rold Kilde	8.31	**Benke 1993**
New Hampshire, USA	Bear Brook	4.29	**Benke 1993**
Denmark	Bisballe Back	23.51	**Benke 1993**
Washington, USA	Snively	14.78	**Benke 1993**
Arizona, USA	Sycamore	141	**Benke 1993**
Arizona, USA	Sycamore	126.27	**Benke 1993**
Washington, USA	Rattlesnake	17.07	**Benke 1993**
Czech Republic	Lusova/Brodska	24.6	**Benke 1993**
New Zealand	Horokiwi	58.96	**Benke 1993**
New Zealand	Horokiwi	25.73	**Benke 1993**
New Zealand	Horokiwi	45.49	**Benke 1993**
New Zealand	Hinau	8.78	**Benke 1993**
New Zealand	Hinau	33.98	**Benke 1993**
New Zealand	Hinau	76.96	**Benke 1993**
Massachusetts, USA	Factory Brook	4.76	**Benke 1993**
Czech Republic	Bityska	111.53	**Benke 1993**
Czech Republic	Bityska	38.58	**Benke 1993**
France	Estaragne	6.51	**Benke 1993**
Minnesota, USA	North Branch	23.51	**Benke 1993**
Virginia, USA	Guys Run	7.31	**Benke 1993**
North Carolina, USA	Upper Ball	8.33	**Benke 1993**
North Carolina, USA	Convict	4.67	**Benke 1993**
Minnesota, USA	Caribou	5.8	**Benke 1993**
South Pacific	Babelboad	7.56	**Benke 1993**
South Pacific	Babelboad	0.69	**Benke 1993**
Minnesota, USA	Blackhoof	7.69	**Benke 1993**
Washington, USA	Douglas	24.22	**Benke 1993**
Wales, UK	Moat-feeder	279.91	**Benke 1993**
South Carolina, USA	Cedar	3.2	**Benke 1993**

Norway	Ekso	3.64	**Benke 1993**
Norway	Ekso	2.44	**Benke 1993**
Norway	Ekso	4	**Benke 1993**
Norway	Ekso	8.6	**Benke 1993**
Norway	Ekso	2.16	**Benke 1993**
Massachusetts, USA	Fort	3.58	**Benke 1993**
France	Nivelle	11.04	**Benke 1993**
Germany	Ilm	45.09	**Benke 1993**
Georgia, USA	Oconee	43.44	**Benke 1993**
Germany	Saale	54.96	**Benke 1993**
Germany	Saale	55.27	**Benke 1993**
Germany	Saale	63.2	**Benke 1993**
Germany	hobbSaale	76.18	**Benke 1993**
UK	Thames	29.02	**Benke 1993**
UK	Thames	18.31	**Benke 1993**
Georgia, USA	Satilla	21.96	**Benke 1993**
Georgia, USA	Satilla	18.73	**Benke 1993**
Georgia, USA	Satilla	67.71	**Benke 1993**
West Virginia, USA	New	639.44	**Benke 1993**
Michigan, USA	St. Marys	14.82	**Benke 1993**
USA, Canada	St. Clair	8.58	**Benke 1993**
USA, Canada	Detroit	6.27	**Benke 1993**
USA, Canada	St. Lawrence	15.56	**Benke 1993**
Japan	Takami	67.07	**Benke 1993**
France	L’Ance du Nord	15.76	**Benke 1993**
Michigan, USA	Shane Creek	1.13	**Entrekin *et al.* 2007**
Michigan, USA	State Creek	2.91	**Entrekin *et al.* 2007**
Michigan, USA	Walton Creek	1.31	**Entrekin *et al.* 2007**
UK	Thames	20	**Mann *et al.* 1972**
Japan	Yoshino	13	**Tsuda *et al.* 1975**
France	Estaragne	5-7.5	**Lavandier 1979**
Denmark	Small stream	25	**Mortensen & Simonsen 1983**
Idaho, USA	Douglas Creek	23.22	**Gaines *et al.* 1992**
Idaho, USA	Snively	14.15	**Gaines *et al.* 1992**
Idaho, USA	Rattlesnake	16.36	**Gaines *et al.* 1992**
Denmark	Rold Kilde	9.54	**Iversen 1988**
North Carolina, USA	Coweeta Catchment 53	13.77	**Lugthart & Wallace 1992**
North Carolina, USA	Coweeta Catchment 54	11.41	**Lugthart & Wallace 1992**
North Carolina, USA	Coweeta Catchment 1985 55	8.79	**Lugthart & Wallace 1992**
North Carolina, USA	Coweeta Catchment 1986 55	10.57	**Lugthart & Wallace 1992**
North Carolina, USA	Upper Ball Creek	7.51	**Huryn & Wallace 1987**
North Carolina, USA	Bear Pen Creek	11.12	**Wohl *et al.* 1995**
Virginia, USA	Buzzard’s Branch	13.92	**Smock *et al.* 1992**
Virginia, USA	Collier’s Creek	5.6	**Smock *et al.* 1992**
New Hampshire, USA	Bear Brook	4.17	**Hall *et al.* 2001**

Maine, USA	Goosefare Brook	27.35	**Woodcock & Huryn 2007**
Maine, USA	West Bear Brook	1.66	**Chadwick & Huryn 2005**
Maine, USA	East Bear Brook	1.68	**Chadwick & Huryn 2005**
Kansas, USA	Kings Creek	19.6	**Stagliano & Whiles 2002**
Kansas, USA	Kings Creek	91.0-319.0	**Whiting *et al.* 2011**
Germany	Steina 1986	19.02	**Meyer & Poepperl 2003**
Germany	Steina 1987	20.83	**Meyer & Poepperl 2003**
Massachusetts, USA	Factory Brook	4.56	**Neves 1979**
New Zealand	Sutton Stream	15.89	**Huryn 1996**
Wisconsin, USA	Sparkling Lake	2-5	**Butkas *et al.* 2011**
UK	River Lambourn	22.6-64.9	**Tod & Schmid-Araya 2009**
China	Tai Po Kau Forest Stream	5.6-7.6	**Dudgeon 1999**
Costa Rica	Sábalo Stream	3.6	**Ramirez & Pringle 1998**
China	Tanqigou Stream	352.8	**Wen *et al.* 2010**
Georgia, USA	Satilla	72.2	**Benke *et al.* 1984**
Georgia, USA	Satilla	28.4	**Benke *et al.* 1984**
Georgia, USA	Satilla	22.0	**Benke *et al.* 1984**
Georgia, USA	Satilla	57.4	**Benke *et al.* 1984**
Georgia, USA	Satilla	13.7	**Benke *et al.* 1984**
Georgia, USA	Satilla	13.9	**Benke *et al.* 1984**
Georgia, USA	Ogeechee River	148	**Benke & Wallace 2014**
Georgia, USA	Ogeechee River	203	**Benke & Wallace 2014**
Georgia, USA	Ogeechee River	48	**Benke & Wallace 2014**
Georgia, USA	Ogeechee River	70	**Benke & Wallace 2014**
Panama	Rio Guabal	30	**Frauendorf *et al.* 2013**
North Carolina, USA	Coweeta Hydrologic Laboratory	116	**Cross *et al.* 2007**

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Chapitre 2: Food-web structure in relation to environmental gradients and predator-prey ratios in tank-bromeliad ecosystems

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Abstract. Little is known of how linkage patterns between species change along environmental gradients. The small, spatially discrete food webs inhabiting tank-bromeliads provide an excellent opportunity to analyse patterns of community diversity and food-web topology (connectance, linkage density, nestedness) in relation to key environmental variables (habitat size, detrital resource, incident radiation) and predators:prey ratios. We sampled 365 bromeliads in a wide range of understorey environments in French Guiana and used gut contents of invertebrates to draw the corresponding 365 connectance webs. At the bromeliad scale, habitat size (water volume) determined the number of species that constitute food-web nodes, the proportion of predators, and food-web topology. The number of species as well as the proportion of predators within bromeliads declined from open to forested habitats, where the volume of water collected by bromeliads was generally lower because of rainfall interception by the canopy. A core group of microorganisms and generalist detritivores remained relatively constant across environments. This suggests that (i) a highly-connected core ensures food-web stability and key ecosystem functions across environments, and (ii) larger deviations in food-web structures can be expected following disturbance if detritivores share traits that determine responses to environmental changes. While linkage density and

nestedness were lower in bromeliads in the forest than in open areas, experiments are needed to confirm a trend for lower food-web stability in the understorey of primary forests.

Key words: biological interactions; ecological networks; ecosystem functions; tank-bromeliads; rainforests; stability

INTRODUCTION

Biodiversity is not only the sum of coexisting species, it is also the diversity of interactions that connect these species. It is widely acknowledged that linkage patterns among species, rather than species richness alone, are a key component of the diversity-stability relationship **(Gilbert 2009)**. For instance, for a fixed number of species, food-web persistence and robustness (two concepts linked to network stability) are believed to increase with connectance, the proportion of all possible interactions that are realized **(Rall *et al.* 2008)**. A rich body of literature has focused on the relationship between network structure and dynamics **(Kondoh 2003)**, and on how different types of interactions (either antagonistic or mutualistic) affect network properties **(Fontaine *et al.* 2011)**. Most studies however focused on network structure regardless of variation in the abiotic environment. Consequently, our understanding of the environmental determinants of network structure lags behind the increasingly vast knowledge of species richness- and interactions-mediated patterns **(Strong *et al.* 1984, Dunne *et al.* 2002)**. Identifying linkages between ecological networks and physical environments could be relevant to predict the extent to which entire communities will respond to increasing environmental disturbances (*e.g.*, climate change, habitat fragmentation, overharvesting, introduction of invasive species, pollution).

On a local scale, both the spatial/temporal changes in habitat conditions and species traits regulate community structure **(Townsend 1989)**, thereby affecting ecosystem functions. For instance, the nature and extent of the riparian vegetation determines food quality and availability in still **(Declerck *et al.* 2006)** and running waters **(Vannote *et al.* 1980)**, thus influencing the functional feeding group composition of macroinvertebrate communities **(Compin & Céréghino 2007)**. However, we know little about how linkage patterns among species (food-web topology) change against a background of environmental gradients over broad, regional scales. Most of what we know about environmental determinants of food-web structure comes from experiments in single locations **(Srivastava & Bell 2009)**, on a target fraction of the food web (*e.g.*, vertebrates, macro- and micro-invertebrates excluding components such as microorganisms, bacteria, flagellates, rotifers and viruses; **Paradise 2004**).

It has proven challenging to study the effects of both abiotic and biotic factors on food webs. High species diversity and population densities in large ecosystems preclude the accurate characterization of trophic links (notably in continuous habitats), and because it is often difficult to manipulate entire ecosystems. To tackle these issues, we focussed on small, spatially discrete food webs that naturally span a broad range of environmental gradients. Bromeliaceae are flowering plants represented by 59 genera and some 3140 species native mainly to the Neotropics **(Givnish *et al.* 2011)**. The interlocking leaves of tank-forming bromeliads form wells that collect water, leaf litter and other organic detritus. The detritus that enter the tank constitute the main source of nutrients for the aquatic food web **(Benzing 2000)**. The aquatic communities inhabiting tank-bromeliads provide excellent opportunities to study food-web structure because they contain several trophic levels (from bacteria to predatory macroinvertebrates; **Brouard *et al.* 2012**) and can be exhaustively sampled **(Romero & Srivastava 2010)**.

The aim of this study was to determine whether spatial patterns in food-web structure can be predicted from a small set of environmental factors and/or the richness of predators relative to their prey. To address this question, we sampled 365 tank-bromeliads in a wide range of environments in French Guiana (plantations, pioneers growths, rock savannah, primary forest) and drew the 365 corresponding food webs using the gut contents of invertebrates as well as observations of predator-prey encounters. Previous studies on tank-bromeliads concluded that detrital resources at the base of the food web, understorey light environments (energy available for algal production), habitat size and predation play key roles in shaping aquatic community composition **(Lounibos *et al.* 1993, Marino *et al.* 2011)**. Detritus constitute the main source of energy for aquatic bromeliad communities, however, the high algal biomass found in sun-exposed bromeliads **(Brouard *et al.* 2011)** may provide a complementary non-detrital resource to the upper trophic levels. If (i) species richness and abundance increase with bromeliad (habitat) size **(Armbruster *et al.* 2002, Jabiol *et al.* 2009, Leroy *et al.* 2009, Céréghino *et al.* 2010, Céréghino *et al.* 2011)**, and (ii) bromeliads from open area benefit from both detrital and non-detrital resources and understorey bromeliad foodwebs are solely supported by detrital matter **(Brouard *et al.* 2012)**, then, for a given habitat size, the diversity of invertebrate functional feeding groups should increase from forest to open areas. One may expect shifts in food-web connectance, linkage density, and/or nestedness as species with particular traits are replaced or complemented by species with other traits when shifting from forest understorey to open areas. Conversely, if the resource that supports food webs does not differ from forest to open areas, then one should not observe significant shifts in food-web structure and functions. To test these hypotheses, we used Linear Mixed Effect modelling to analyse patterns of community diversity and food-web topology in relation to key environmental variables and predator:prey richness ratios.

MATERIAL AND METHODS

Ethics Statement

This study was conducted according to relevant national and international guidelines. Sample collections necessary to scientific research were authorized by the French *Office National des Forêts* (ONF) provided that their impact upon the environment is considered negligible.

Study area, bromeliads and environmental variables

The study was conducted in French Guiana, from March 2006 to October 2011. The climate is tropical moist with 3,000 - 3,400 mm of yearly precipitation mainly distributed over 280 days. There is a major reduction in rainfall between September and November and another shorter and more irregular dry period in March. The maximum monthly temperature averages 33.5° C (32.1-35.8°C), and the monthly minimum averages 20.3°C (19.7-21°C).

We selected five sampling localities distributed across a south-east to north-west range (Figure 2.1) and sampled 365 bromeliads (*i.e.,* 365 food webs) in the understorey of primary and transitional forests, in pioneer growths, in a rock savannah, and in plantations. The main habitat characteristics of tank-bromeliad species found in five vegetation types at five localities (hereafter "vegetation types", within localities) are summarized in Table 2.1. Further descriptions of the Nouragues (sampling period in April 2006), Petit-Saut (March 2009) and Kaw (Oct. 2008) localities and their bromeliads can be found in **(Bongers *et al.* 2001, Céréghino *et al.* 2011, Brouard *et al.* 2012)**. Saint-Elie (Oct. 2007) and Angoulème (April 2010) are *Citrus* plantations. Both epiphytic bromeliads and those that had taken root on the ground were included in the study.

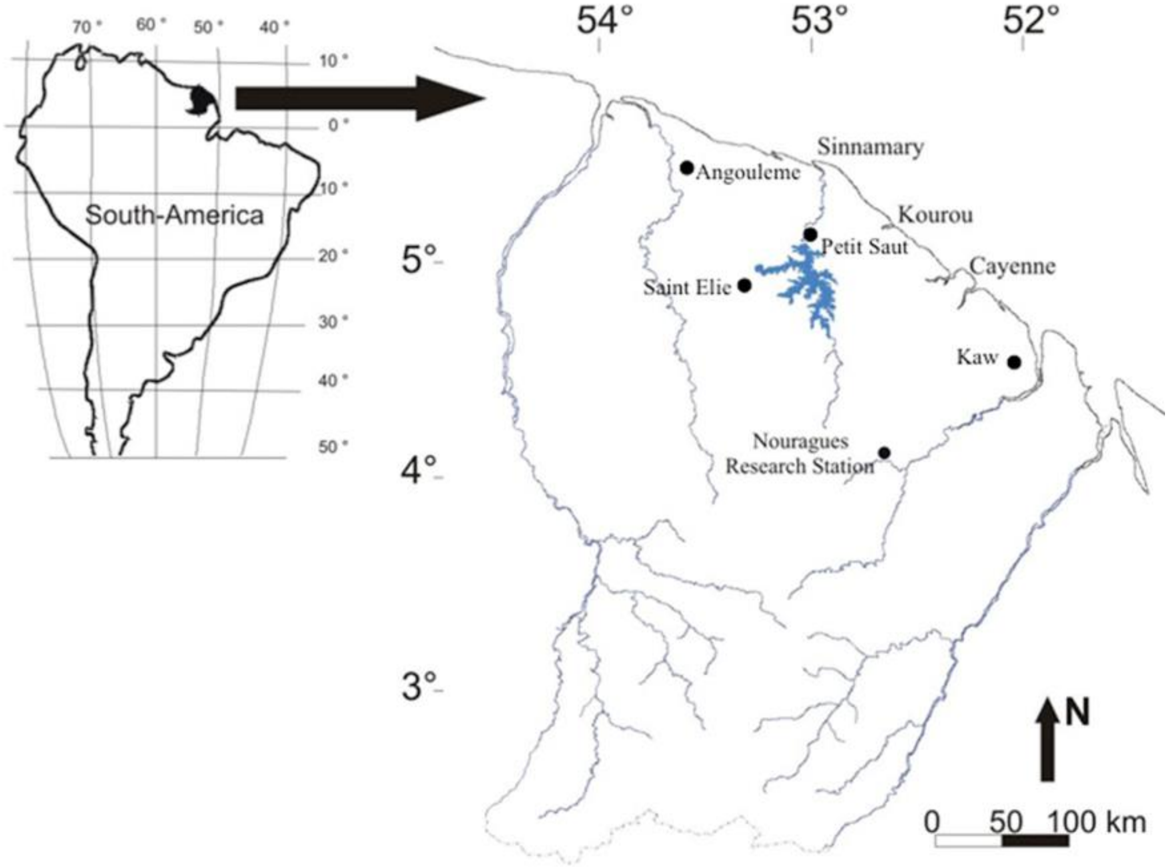

Figure 2.1 Distribution of the sampling locations in French Guiana (see Table 2.1)

Table 2.1 Main habitat characteristics (mean±standard error) of tank-bromeliad species found in five vegetation types. CB: C. berteroniana*; AA:* A. aquilega*; VP:* V. pleiosticha*; AB:* A. bromeliifolia*; VS:* V. splendens*; GL:* G. lingulata*; AM:* A. mertensii. *N = number of plants sampled, IR = incident radiation (%), WV = water volume extracted (mL), FPOM = fine particulate organic matter (mL after decantation in test-tubes), #Taxa = number of taxa per food web.*

Locality	Vegetation types	Species	N	IR	WV	FPOM	#Taxa
Nouragues	Rock savannah	CB	29	73.3±2.4	40.62±3.75	0.74±0.08	10.55±0.15
		AA	31	66.97±2.73	949.23±102.64	10.84±1.26	15.87±0.42
	Transitional forest	VP	30	25.12±0.29	73.2±9.11	1.7±0.28	10.3±0.35
		AB	26	25.69±0.47	137.85±21.1	1.08±0.25	11.23±0.32
	Primary forest	VS	26	18.75±0.4	48.54±5.03	4.29±0.42	10.35±0.25
		GL	19	15.9±0.6	17.46±2.53	1.04±0.16	9.21±0.29
Petit-Saut	Pioneer growth	AM	63	39.33±2.63	84.38±10.1	6.16±1.26	12.49±0.28
	Primary forest	VS	34	16.64±0.38	26.18±3.84	3.46±0.71	10.68±0.23
Kaw	Pioneer growth	AM	45	35.1±2.98	92.46±11.82	4.3±0.68	11.78±0.28
Angoulème	*Citrus* plantation	AM	35	33.03±2.95	31.01±4.54	2.32±0.31	11.8±0.34
Saint-Elie	*Citrus* plantation	AM	27	32.07±1.3	56.41±8.29	4.58±0.86	14.22±0.36

In order to prevent seasonality effects (*i.e.*, dry *vs* rainy season) on water volumes and species abundance, the sampling took place at the transition between rainy and dry seasons, where invertebrate abundances reach a peak. We also sampled tank-bromeliads that were full of water. Species occurrence was not an issue as bromeliad invertebrates have fast life cycles

(< 2 months) with overlapping cohorts. To characterize habitat size, we emptied the wells in each plant by sucking the water out (see invertebrate sampling) and recorded the corresponding volume of water (WV, mL). The amount of fine particulate organic matter (FPOM; 1000 to 0.45 µm in size) was expressed as preserved volume (mL) after decantation in graduated test-tubes **(Paradise 2004)**. Finally, percentages of total incident radiation (IR) above the bromeliads were calculated using hemispherical photographs and an image processing software (Gap Light Analyzer 2.0; **Frazer *et al.* 1999**), as described in **(Leroy *et al.* 2009)**. In this study, we consider that all bromeliads with an IR below 50% were located in partially shaded areas or forested environments while higher percentages defined sun-exposed areas.

Aquatic invertebrate communities

For both ethical (extensive sampling could destroy local populations) and legal reasons (the Nouragues Research Station is located in a nature reserve), we decided to use a non-destructive sampling technique for all studied bromeliads. To sample the water retained in the tanks, we used 5-mL and 10-mL automatic micropipettes with the end trimmed to widen the orifice. We homogenized the water within leaf wells by sucking in and out with a pipette, before sucking out the content. Although less efficient than plant dissection, we and other researchers have already successfully used this technique **(Céréghino *et al.* 2010, Jocqué *et al.* 2010)**. It was consistently used for all of the samples and most of the water (>95%) was collected. Both early and late instars of prey and predator invertebrates were captured, so we were confident that our technique was efficiently implemented. The samples were preserved in the field in 4% (final concentration) formalin. Invertebrates were sorted in the laboratory and preserved in 70% ethanol. They were identified to genus, species or morphospecies and enumerated (species lists in **Jabiol *et al.* 2009, Céréghino *et al.* 2010**). Species abundance data (individuals per plant) were used to calculate evenness (Simpson index) and entropy (Shannon-Weaver index) for each invertebrate community. The Simpson index was calculated as $D = \Sigma\ p_i^2$. The Shannon-Weaver index (hereafter Shannon index) was defined as $H = -\Sigma\ p_i \log(b)\ p_i$, where p_i is the proportional abundance of species i and b is the base of the logarithm (natural logarithm in this case). Species richness and abundance being components of these two indices, they were not considered alone in subsequent modeling. Macroinvertebrate taxa were partitioned into predators (carnivorous species which attack and consume living macroinvertebrates) and prey (species which sift fine particulates and microorganisms from the water column and/or gather FPOM and associated microorganisms from the accumulated debris), and these categories were used to calculate Predator:Prey Richness ratios (number of predatory taxa/number of prey taxa, hereafter PPR).

Food web characterization

The diet of the various invertebrate species that make up food webs was determined by dissecting the entire guts. Twenty to 50 individual guts from each taxon were dissected across both localities and vegetation types in order to encompass the variability in diets of omnivores and predators. The gut contents of predators were placed into a drop of water on a glass slide, spread out, and analysed using a binocular microscope (Leica® MZ 12.5) and an Optiphot-2 Nikon® microscope whenever necessary. Most of the prey items could be identified from the guts of predators by comparing the chitinous parts (head capsules or legs, setae…) with specimens of bromeliad invertebrates archived in our collection (Univ. of Toulouse III). Only the gut contents of piercers (Heteroptera Veliidae, Diptera Tabanidae) could not be identified visually; in this case, we relied on observations of arranged encounters in test tubes.

The microorganisms found in the guts of detritivores were identified to a coarse taxonomic level using an Optiphot-2 Nikon microscope at x600 magnification. Determinations were based on earlier descriptions **(Carrias *et al.* 2001, Carrias *et al.* 2012)**, and on recent microbiological samples (unpublished data). The presence of particulate organic matter was also recorded in the gut contents, and we used an ocular micrometer to distinguish fine particulate organic matter (FPOM, 1000 to 0.45 µm in size) from coarse particulate organic matter (CPOM, >1000 µm). Gut contents and other observations were used to build 365 interaction matrices (one per bromeliad) that described 365 "connectance webs" *sensu* **Post 2002b**; see Figure 1.1).

Three topological descriptors were used to describe food webs: connectance, linkage density, and nestedness. In the literature, two measures of the connectance are widely used: connectance and normalized connectance. Both refer to the proportion of all possible interactions that are realized, but normalized connectance is rather used for food webs comprising less than 20 species **(Gilbert 2009)**. However, in this study, the two measures were strongly correlated (Pearson's correlation coefficient = 0.966, $p<0.0001$) and we therefore used the connectance as defined by **(Morin 1999)**:

$$C = \frac{2 \times Links}{Species \times (Species - 1)}$$

Linkage density was calculated as the ratio between the number of links and the number of species. Levels of nestedness were expressed as matrix temperatures, with values ranging from 0 (perfectly nested) to 100 (see **Bascompte *et al.* 2003**) were calculated from the 365 interaction matrices (binary data) using the BINMATNEST3 program **(Rodríguez-Gironés & Santamaría 2006)**. Departure from random was tested against a number of 1000 random matrices using the most conservative null model in BINMATNEST3 (namely "model 3"). A matrix temperature is affected by both its structure (the fill) and its size (the number of rows and columns). The extent to which the observed temperature departs from random depends on how random matrices are built. Unlike the null models 1 and 2, the model 3 is a packing algorithm that generates random matrices that are less influenced by the structure of the input matrix, thus allowing for comparisons with other studies **(Rodríguez-Gironés & Santamaría 2006)**. More specifically, the null model 3 generates random matrices where each cell has a probability of containing a "1" equal to the averaged probability of occupancy of rows and columns of the input matrix. Therefore, the fill of each cell depends on both the fraction of "1s" in rows and columns in which the cell is included.

Data analysis

To analyze the relationships between food-web descriptors, environmental variables and PPRs, we used linear mixed effect modeling. All variables were log-transformed to fit a normal distribution. Because a given vegetation type was found at only one locality, we qualified this structure as the "vegetation type nested within locality". In contrast, a given bromeliad species could be sampled at many localities or many vegetation types, therefore the variable "bromeliad species" was not nested within the former or the latter. Since "locality", "vegetation type", "vegetation type nested within locality" or "bromeliad species" could be included as random factors, we performed a model selection based on the more conservative Bayesian Information Criterion (BIC) of the full models (models considering all environmental variables) for each dependent variable. Then, for a selected random factor (the remaining random effects being dropped from the model), the relationship between dependent and independent variables were explored using a stepwise backwards removal procedure and only the final models containing significant variables were presented. Departures from homoscedasticity and the normality of the residual errors were evaluated graphically for each final model. All statistical analyses were evaluated under a 95% confidence level and were conducted using R software V. 3.2.1 **(R Core Team 2015)** and the associated packages for Linear Mixed Effect Modeling (nlme, lmer4).

RESULTS

Abiotic environments and food-web composition

There were large differences in WV and FPOM among bromeliad species, even at a given vegetation type (Table 2.1). The two bromeliads growing in rock savannah (*A. aquilega* and *C. berteroniana*) showed the highest and lowest mean values for FPOM (10.84 mL *vs*. 0.74 mL, respectively), and the highest and one of the lower mean values for WV (949.23 mL *vs*. 40.62 mL, respectively) compared to the others tank-bromeliad species. Thus, even though the understorey of primary forests consistently received lower incident radiation (*i.e., V. splendens* and *G. lingulata*) and higher litter inputs than sun-exposed areas, the amount of FPOM inside the tank of bromeliads from primary forests was not necessarily higher than those from rock savannah. However, bromeliads from primary forests had higher FPOM:WV ratios (0.05-0.09 mL FPOM/mL WV) than bromeliads from open areas (0.01-0.02 mL FPOM/mL WV).

Food webs comprised 8 to 20 taxa (median = 11 taxa), including macroinvertebrates, rotifers, and miscellaneous microorganisms (bacteria, cyanobacteria, fungi, algae, heterotrophic flagellates, and ciliates) identified in the gut contents. The predators belonged to the Diptera Culicidae (*Toxorhynchites purpureus*), Corethrellidae (*Corethrella* sp.) and Tabanidae, and to the Odonata (one unidentified Coenagrionidae species). Detritivores mostly consisted in Diptera Culicidae (*Culex* spp. and *Wyeomyia* spp.), Limoniinae, Chironomidae (*Tanytarsus* sp.) and Psychodidae (*Telmatoscopus* spp.). The list of taxa and the corresponding functional groups is provided in Figure 2.2.

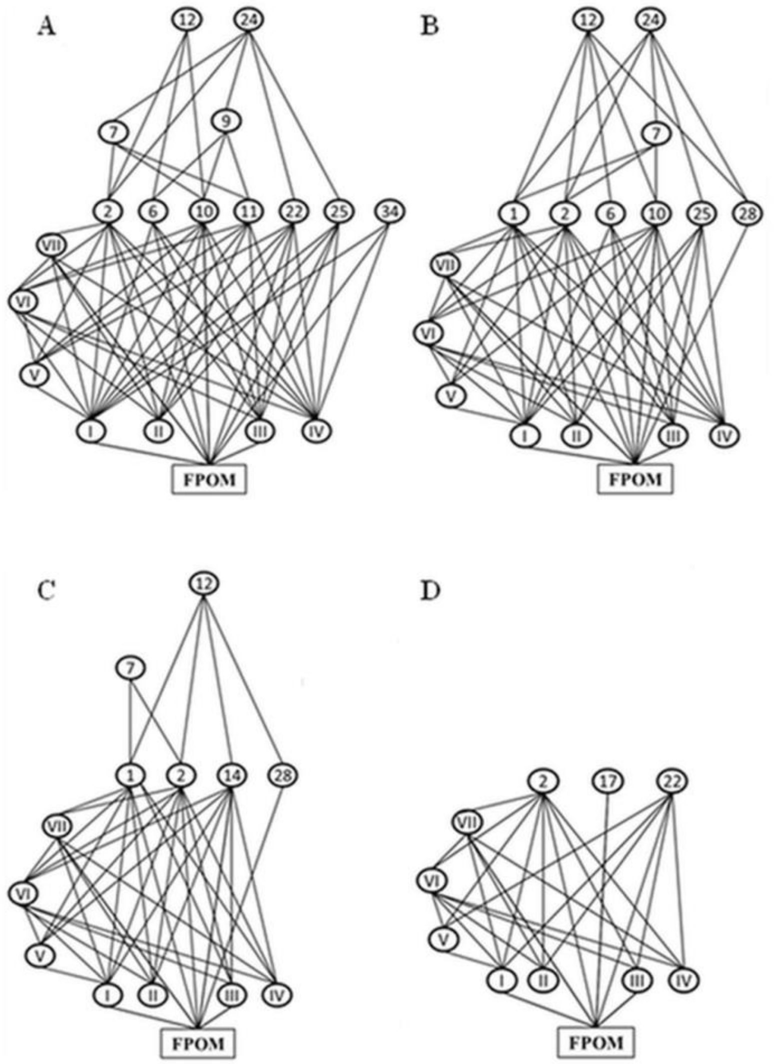

Figure 2.2 Examples of connectance webs under two contrasted environmental conditions: open areas (A, B) and forest areas (C, D). The upper trophic level (predators) is at the top of the graphs, and the lower (algae, detritus) at the bottom. Numbers and abbreviations are for: Wyeomyia *spp. (1; filter-feeder);* Culex *spp. (2; filter-feeder); Forcypomiinae sp2 (6; filter-feeder);* Bezzia *sp. (7; predator); Tanypodinae (9; predator); Chironominae (10; detritivore); Tanytarsinii (11; detritivore);* Corethrella *sp. (12; predator);* Telmatoscopus *sp1 (14; detritivore); Limoniinae (17; detritivore-shredder);* Cyphon *sp. (22; shredder); Coenagrionidae (24; predator);* Aulophorus superterrenus *(25; detritivore); Hydracarina (28; detritivore);* Elpidium *sp. (34; detritivore-scraper); Bacteria (I); Cyanobacteria (II); Fungi (III); Algae (IV); Flagellate (V); Ciliate (VI); Rotifera (VII); Fine Particulate Organic Matter (FPOM).*

Model selection and influence of abiotic and biotic variables on food webs

All random factors were selected in at least one model (Table 2.2), suggesting that different spatial scales could provide complementary explanations to the observed pattern. More specifically, “vegetation type” and “bromeliad species” were included as random factors in the Simpson index (BIC = -314.16) and connectance models (BIC = -1108.648), respectively. “Locality” was selected in the Shannon index, linkage density and nestedness models (BIC = 21.83, BIC = -586.99, and BIC = -546.25, respectively). The subsequent stepwise backward removal procedures for each food-web descriptor were thus performed using their selected random factors. The computation of likelihood ratios demonstrated that we could not discriminate the model with “locality” from the one with “vegetation type” as random factor for the Shannon index model (L = 0.034, *p* = 0.92). Therefore, the variable selection for the Shannon index model was also performed with “vegetation type” as random factor. In general, the inclusion of random factors with higher BIC values (*e.g.,* “vegetation type”, “vegetation type nested within locality” or “bromeliad species”) only slightly affected the outcomes of the models in terms of significant and non-significant interactions among variables. More specifically, interactions that were barely significant with the selected random factor became non-significant when other random factors were included.

Table 2.2 Bayesian Information Criterion (BIC) of the full models with four different random effects for each food-web descriptor. The random effect ‘Locality/Vegetation type’ means that the vegetation types are nested within the localities. Bold characters highlight the lowest BICs.

Models	**Random effects**			
	Vegetation type	Locality	Locality/Vegetation type	Bromeliad species
Shannon-Weaver’s index	21.87	**21.83**	25.79	31.69
Simpson’s index	**-314.16**	-310.39	-308.73	-310.19
Connectance	-1102.57	-1090.4	-1097.89	**-1108.65**
Linkage density	-584.88	**-586.99**	-582.41	-564.51
Nestedness	-544.09	**-546.25**	-541.21	-527.14

The Shannon and Simpson indices were both positively correlated with WV ($p<0.0001$) and with PPR ($p = 0.0009$ and $p = 0.0027$, respectively; Table 2.3), showing that invertebrate community diversity increased with habitat size and the relative number of predators. Moreover, these two models showed a negative interaction between FPOM and PPR ($p = 0.036$ and $p = 0.047$, respectively). However, when “vegetation type” was included as random factor in the Shannon index model, both water volume and PPR remained significant but the FPOM:PPR interaction was not significant ($p = 0.081$). Last, the variable “IR” was not significantly correlated with the Shannon index, whatever the random factor included ($p = 0.6 – 0.75$). Finally, the two negative interactions IR:WV and PPR: FPOM become significant ($p = 0.046$ and $p = 0.014$, respectively) for the Simpson index when “Locality” was included as a random factor.

Connectance showed a negative and significant correlation with WV and PPR ($p = 0.0079$ and $p<0.0001$, respectively), and there was a trend for decreasing connectance with increasing FPOM amount ($p =0.039$; Table 2.3). Incident radiation was not significantly correlated with connectance (*p* = 0.24). When "Locality" was included, the two negative interactions IR:WV and WV:FPOM turned to be significant (*p* = 0.0002 and *p* = 0.009, respectively) in the connectance model. Both the linkage density and nestedness models showed a significant negative interaction between WV and IR (*p* = 0.008 and *p* = 0.0071, respectively). Linkage density and nestedness were positively correlated with WV and IR, and negatively correlated with PPR (Table 3). Linkage density was positively correlated with the IR:FPOM interaction (*p* = 0.034) , but did not correlate with FPOM alone (*p* = 0.064). Finally, levels of nestedness (*N*) ranged from 21.54 to 49.79 (median *N* = 39.98). Overall, 44.4% of our interaction matrices were significantly different from the null matrices obtained at random (*p* = 0.0001 to 0.99, median *p* = 0.08). Nevertheless, this percentage increased with the number of taxa; for instance, 66.1% and 88.8% of all of the interaction matrices comprising ≥13 and ≥17 taxa, respectively, were significantly different from random.

Table 2.3 Models evaluating the patterns of community diversity (Shannon's entropy and Simpson's evenness) and food-web structure (connectance, linkage density, nestedness) in relation to environmental variables and their interactions. IR = %incident radiation, WV = water volume (mL), FPOM = fine particulate organic matter (mL), PPR = Predator:Prey Ratio (see text). Only variables and interactions with p<0.05 are interpreted as statistically significant and presented in the table.

Fixed Effects	Estimate±SE	t-value	df	*p*	Random Effects
Shannon					Locality
Intercept	0.296±0.068	4.305	356	<0.0001	
Slope					
WV	0.091±0.011	7.72	356	<0.0001	
FPOM	0.044±0.025	1.773	356	0.077	
PPR	0.268±0.08	3.357	356	0.0009	
FPOM:PPR	-0.126±0.059	-2.103	356	0.036	
Simpson					Vegetation type
Intercept	0.226±0.036	6.157	352	<0.0001	
Slope					
WV	0.04±0.008	4.889	352	<0.0001	
FPOM	0.02±0.016	1.226	352	0.22	
PPR	0.15±0.049	3.025	352	0.0027	
FPOM:PPR	-0.074±0.037	-1.992	352	0.047	
Connectance					Bromeliad species
Intercept	0.60±0.017	35.018	355	<0.0001	
Slope					
WV	-0.007±0.002	-2.671	355	0.0079	
FPOM	-0.007±0.003	-2.07	355	0.039	
PPR	-0.14±0.009	-15.039	355	<0.0001	
Linkage Density					Locality
Intercept	1.136±0.102	11.117	354	<0.0001	
Slope					
IR	0.079±0.027	2.85	354	0.0046	
WV	0.141±0.029	4.77	354	<0.0001	
FPOM	-0.087±0.047	-1.854	354	0.064	
PPR	-0.186±0.019	-9.365	354	<0.0001	
IR:WV	-0.028±0.008	-3.4	354	0.008	
IR:FPOM	0.028±0.013	2.124	354	0.034	
Nestedness					Locality
Intercept	3.302±0.107	30.664	355	<0.0001	
Slope					
IR	0.087±0.029	3.014	355	0.0028	
WV	0.106±0.025	4.126	355	<0.0001	
FPOM	0.02±0.007	2.619	355	0.0092	
PPR	-0.237±0.021	-11.204		<0.0001	
IR:WV	-0.019±0.008	-2.708	355	0.0071	

DISCUSSION

Based on an unprecedented number of replicates under natural conditions, our models have proven informative in assessing whether environmental factors and biological interactions explain some patterns of food-web structure. Overall, variations in food-web structure across environments and spatial scales were mostly due to interactions between habitat size and the distribution of predators (Kendall's test, positive correlation between WV and PPR, $\rho = 0.179$, $p<0.0001$). There was however a trend for more feeding links in open areas compared to forest understorey. Finally, a core of generalists remained relatively constant across large regional scales, so that patterns of food-web connectance, linkage density and nestedness were mostly related to the addition or loss of predators.

Water volume was one of the most significant variables in all models, suggesting that habitat size was the primary factor controlling species composition and abundance patterns and, subsequently, food-web structure. Larger habitats are more easily colonized by immigrants, resulting in positive species-area relationships **(Drakare *et al.* 2006)**. An increase in habitat area also fosters functional diversity **(Takimoto & Post 2012)**, while allowing for a better partitioning of food resources by coexisting species **(Richardson *et al.* 2000b)**. Hence, at any given locality, both the number of taxa and individuals per plant increased with habitat size (there was a positive correlation between WV and PPR, Kendall's test = 0.179, $p< 0.0001$), which is consistent with previous findings on bromeliad ecosystems **(Jabiol *et al.* 2009)** and small wetlands in general **(Oertli *et al.* 2002)**. However, there was a trend for bromeliad with higher incident radiation to accumulate more water (positive WV to IR relationship, $r = 0.32$, $p< 0.05$, log-transformed data) certainly because in open areas there are fewer overhanging trees to keep most of the rain from reaching the bromeliads. Indeed, based on measures made in the understorey of the primary forest in Petit-Saut, we estimated that 30-38% of the rain is intercepted by the canopy. Hence, for a given bromeliad species and size, the containers hold more water at sun-exposed areas. Nevertheless, the complex interaction between habitat size and incident radiation (significant interaction between IR and WV in the linkage density and nestedness models, but not in the connectance model) precludes a precise distinction of their relative impacts on food webs. We cautiously suggest an indirect effect where IR mediates food-web features through bromeliads' carrying capacity for aquatic invertebrates.

In aquatic ecosystems, detrital inputs form a strong trophic link between plant production, decomposer microorganisms, and larger metazoans **(Vondracek *et al.* 2005)**. In tank-bromeliads, detritus constitutes the main source of nutrients for the aquatic food web **(Benzing 2000)**. Debris-chewing invertebrates process incoming litter. Small particles, including faeces, are then washed into the plant pools where the FPOM is further processed in the gut of invertebrate collectors and filterers. Dead organisms, litter, and faecal particles, which collect in the leaf bases, are utilized by bacteria and other microorganisms. The nature and extent of the vegetation that surrounds these systems was therefore expected to have a strong influence on food-web structure through food quality and availability. On one hand, algae were found to account for more than 30% of the total microbial diversity and biomass in sun-exposed bromeliads **(Brouard *et al.* 2011, Marino *et al.* 2011)**, which usually receive lower amounts of leaf litter **(Brouard *et al.* 2012)**. We suggest that such a complementary "green" food web could contribute to reducing functional redundancy in FPOM-poor systems. Overall, there was a positive correlation between WV and FPOM (Kendall's test = 0.349, p< 0.0001). However, higher FPOM concentrations (*i.e.,* the amount of FPOM in relation to WV) decreased the amount of open water inside of the tank, which had a negative effect on aquatic organism diversity. High FPOM concentrations may have the effect of clogging habitats in small freshwater ecosystems and, to a certain extent, space availability **(Jabiol *et al.* 2009)**. Since FPOM was not consistently significant in our models, we assume that resource availability is not a limiting factor in bromeliad systems. However, the influence of resource quality (detritus *vs*. algae) on individual food apportionment should deserve more attention in future studies.

The PPR was a highly significant variable in all models. Connectance, linkage density and nestedness (matrix temperature) significantly decreased with increasing proportions of predators. A decrease in connectance and linkage density can be due to a gain of specialists and/or a loss of generalists **(Gilbert 2009)**. In our study, predators were generalist species in that they fed on numerous prey species and multiple trophic levels, but they could be considered as "node specialists" since they interacted mainly with their prey while prey established links with both basal species (algae, rotifers, ciliates...) and predators. The extent to which predators are specialized on specific prey plays a great role in generating patterns of community diversity from site-to-site to large regional scales **(Chase *et al.* 2009, Ryberg *et al.* 2012)**. We found that the Shannon and Simpson indices (entropy and evenness, respectively) were positively correlated with the PPR at relatively small scales (from individual bromeliads to local scales), but overall, bromeliad food webs comprising less than 13 species were primarily composed of microorganisms and primary consumers, and were characterized by high levels of diffuse interactions where all species were more or less closely linked to each other. Indeed, a core of highly-connected species remained relatively constant at lower trophic levels (see also **Valladares *et al.* 2012**), both in terms of species identity and ecological function, between individual bromeliads and from open to closed areas. For instance, the dominant generalist detritivores belonging to the Culicidae (*Wyeomyia* sp., *Culex* sp., and *Anopheles* sp.), Chironomidae and Oligochaeta were found in 310, 215 and 133 plants out of 365 respectively. The main top-predators, namely Corethrellidae, Ceratopogonidae and *Toxorhynchites* sp., occurred in 122, 105 and 83 plants respectively. It is likely that this highly-connected core ensures food-web stability and key ecosystem functions (*e.g.*, decomposition, nutrient cycling) across environments. If detritivores share traits that determine responses to environmental changes in any given area (*e.g.*, resistance to dessication, dispersal ability), then larger deviations in food-web structures can be expected following a major disturbance. Beyond 13 species, community diversity and food-web nestedness increased as a result of the addition of specialist predators and generalist detritivores. Our observations suggest that predators could enter the food webs at an average water volume of 49.9 mL, which corresponded to 1 predator species for 3 prey species on average. Regardless of the locality, larger bromeliad hosted a higher proportion of predators. In addition to their intrinsic value for biological diversity, predators (*i.e.*, *Toxorhynchites* sp., *Corethrella* sp. and Coenagrionidae) thus played a key role in generating food-web patterns. This assumption is supported by the fact that, whilst predators are less frequent than detritivores, the predator:prey ratio was a significant variable in all three food-web topology models (connectance, linkage density and nestedness). We suggest that the addition of species at higher trophic levels contributes to departure from random interactions through the partition of prey resources between coexisting predators. Our results are also in line with studies which demonstrated that specialized species tend to be dependent on a core of densely connected generalist species, and that natural communities display non-random interaction patterns **(Bascompte *et al.* 2003, Fox 2006, Bascompte 2009, Fontaine *et al.* 2009)**. Therefore, although we relied on unweighted trophic links to analyse spatial patterns in food-webs, this study provides strong empirical support on how food-web structure change along environmental and predator richness gradients. We conclude that at the bromeliad scale, habitat size determines the number of species that constitute food-web nodes and the proportion of predators (positive relationship), and subsequently, food-web topology. Hence, the number of species as well as the proportion of predators within assemblages globally decline from open to closed (forest) habitats, where the volume of water collected by bromeliads is generally lower because of rainfall interception by the canopy. The extent to which stability is related to linkage patterns (notably nestedness) in networks such as food webs remains however unclear and obviously deserves further research **(Tylianakis *et al.* 2010)**. While linkage density and nestedness were lower in forested areas, experimental research is now needed to confirm a trend for lower food-web stability in the understorey of primary forests.

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Chapitre 3: Are trophic pathways predictable across broad biogeographic scales?

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Abstract. Although, at a local scale, trophic pathways are known to be influenced by environmental factors, trophic structure, and species diversity, there have been few attempts however to investigate the ubiquity and consistency of trophic pathways over broad biogeographic areas. We evaluated the relative contribution of different functional feeding groups to the diet of consumer species living in the interlocking leaves of tank bromeliads. We sampled bromeliads growing in either open or shaded habitats, within three distant regions from Central to South America in order to disentangle the effects of regions, habitats, and top-down processes at shaping trophic pathways. All functional feeding groups were consistently found across the latitudinal gradient thus ensuring key ecosystem functions. The significant interaction between habitats and regions suggests that the variability in trophic pathways could be explained by site-specific differences in prey composition and by the opportunistic predatory behavior of odonate larva. This observation is partially confirmed as predators tracked shifts in prey biomass in one study site (Costa Rica). Despite this variability, shredders seem to be preferentially consumed by predators whereas gatherers escape, to some extent, the predation pressure, a result consistently observed across the spatial gradient. This study suggests that global changes by disproportionately affecting large bodied predators may have critical impacts on decomposition processes and nutrient cycling through indirect interactions and strong top-down processes. Additionally, local environmental factors are likely to be as important as broad-scale biogeography and climate in driving food-web patterns.

Keywords: energy flow; biogeography; top-down control; trophic structure; tank bromeliads

INTRODUCTION

Surveys of animal communities have shown that the way energy flows within faunal food webs is quite predictable at small to medium spatial scales **(Guzzo *et al.* 2011)**, where trophic pathways are largely determined by a combination of environmental filtering and biological interactions within the community, that shape species diversity and the relative abundance of various trophic guilds. This is particularly well illustrated, for instance, by river invertebrate communities **(Vannote *et al.* 1980)**. Typically, in upland streams surrounded by dense forest, shredders reduce coarse particulate organic matter to fine particulate organic matter, making it available to collectors. Photosynthesis is higher in streams flowing in open areas where proportions of shredders fall due to lower inputs of riparian coarse particulate organic matter, and grazer-scrapers are more abundant due to higher algal production. We however miss analyses of the consistency of trophic pathways at much larger spatial scales, where species show important biogeographic turnover in composition and traits **(Vanderklift & Wernberg 2010, Jardine 2014, Kimbro *et al.* 2014)**. Moreover, entire taxonomic groups that exploit particular food resources may be entirely absent from some regions / countries, due to different biogeographic histories. For instance, Plecoptera, an important insect clade mostly comprising shredders and predators in most rivers worldwide, are absent in Caribbean islands, Macaronesia (Atlantic Ocean) and the Reunion (Indian Ocean), and are scarce in the Guyana Shield (South-America; **Stark 2000, Dedieu *et al.* 2015**). One may therefore expect that such changes in the abundance or presence of important predatory and/or detritivorous species along broad latitudinal gradients will have pervading effects upon the entire food chain **(Andrew & Hughes 2005)**, and that the extent of both top-down and bottom-up effects will be modulated by local environmental conditions that determine the main sources of energy for the food webs (detritus in closed forest habitats, detritus and primary production in more open habitats). For example, in detritus-based food webs, predators were found to adversely affect the abundance of decomposers (thus lowering decomposition rates), while in primary production-based food webs, the same predators suppressed herbivores thereby fostering plant growth **(Wu *et al.* 2014)**. In summary, integrated analyses of trophic pathways that include comparisons between habitats and "countries" are much needed to assess the extent to which food web structure is mediated by biological interactions, physical properties of habitat structure (local processes) and/or by dispersal limitations (*e.g.,* physical barriers, insular contexts) or biogeographic history (regional processes).

It has been challenging to collect data on food webs over broad spatial scales in a standardized manner, first because many food webs are too complex or spatially diffuse to allow adequate sampling, and second because most ecosystem types lack natural replication. The faunal food web within "tank" bromeliads (Bromeliaceae) allows to tackle these issues in that it is small and contained (allowing complete sampling of the macroorganisms), widely distributed and highly replicated in nature (allowing to test the generality of results over a broad biogeographic gradient). Owing to these features, tank-bromeliads and their aquatic biota are ideal model systems for studies of many basic ecosystem processes **(Srivastava *et al.* 2004)**, ranging from the rules by which communities and food webs are assembled **(Petermann *et al.* 2015)** to the relationships between diversity and ecosystem function **(Leroy *et al.* 2009, Srivastava & Bell 2009)**. Bromeliads are flowering plants represented by 3140 species native mainly to the neotropics **(Givnish *et al.* 2011)**. In rainforests, tank-bromeliads can impound up to 50,000 liters of water per hectare **(Sugden & Robins 1979, Richardson 1999)**. Their rosettes collect rainwater and leaf litter and provide a habitat for aquatic organisms ranging from prokaryotes to invertebrates **(Frank & Lounibos 2009, Brouard *et al.* 2012)**. Macroinvertebrates, mostly aquatic insect larvae, constitute the dominant part of animal biomass within bromeliad ecosystems. Interestingly, geographic patterns of bromeliad-associated diversity parallel that of most terrestrial species in the Neotropics **(Gentry & Dodson 1987)**. The detritus constitutes the main source of nutrients at the bottom of the aquatic food web. Incoming litter is reduced by invertebrate shredders and scrapers, then small particles of organic matter and faeces collect in the plant pools, where particulate organic matter is further processed in the gut of collectors and filterers, and utilized by bacteria and other microorganisms **(Ngai & Srivastava 2006)**. Although it is broadly accepted that tank-bromeliads growing in closed forest understories host a detritus-based food web **(Kitching 2000)**, recent studies by **Marino *et al.* (2011)** and **Brouard et al. (2011, 2012)** strongly suggest that algal production supports a complementary, non-detrital food web in sun-exposed bromeliads. Bromeliad food webs are thus relevant to investigate changes in trophic pathways along both habitat and biogeographic gradients.

Whilst the importance of the “brown” (detritus) and “green” (algae) sources in bromeliads influences the diversity and abundance of primary consumers (*i.e.,* shredders, collectors, filterers), bromeliad food webs are also strongly controlled by predation by large-bodied insect larvae such as damselfly odonates and/or *Toxorhynchites* culicids which reduce the abundance of prey, and thus have indirect impacts on processes such as decomposition **(Yanoviak 1999, Yanoviak 2001b)**. Gut content analyses showed that these species feed on all invertebrates available **(Dézerald *et al.* 2013)**, making them generalist predators **(Petermann *et al.* 2015)**. Hence, both local habitat conditions and biogeographic location are likely to influence predators’ diets, thereby affecting patterns of energy flow and top-down controls of communities in bromeliad ecosystems.

In this study, we aimed at quantifying the variability in predators’ diet and top-down control in bromeliad food webs, to determine whether general trophic pathways can be identified in by habitats and/or across large spatial scales. Stable isotope analyses are based on the predictable relationship between the isotopic composition of consumers and their diet, and are thus a sensitive and temporally integrative tool to analyse long-term dietary records in animal tissues **(Post 2002a)**. Stable isotope analyses were used to evaluate the relative contribution of different macroinvertebrate functional feeding groups to the diet of predatory aquatic larva (Odonata; as a functional feeding group) in open and closed habitats at three sites ranging from 18°N to 25°S in the neotropics (Brazil, Costa Rica and French Guiana). We focused on Odonates, because these top-predators are widely distributed and they can represent an important fraction of predators’ biomass in bromeliads **(Petermann *et al.* 2015)**. This study thus aimed at partitioning the relative influence of “habitat” and “sites” in modulating the influence of top-down control on trophic pathways. Assuming that, at local spatial scales, Odonates tend to show higher abundances in sun-exposed bromeliads **(Brouard *et al.* 2012)** whereas prey species composition shows a rapid turnover at broader scales **(Srivastava 2005)**, we hypothesized the trophic pathways to be predictable from habitats to distant sites only if predators consistently track shifts in prey relative biomass.

MATERIALS AND METHODS

Sampling sites

Samples were taken at three sites distributed along a latitudinal gradient ranging from 18°N to 25°S. There was one site in Costa Rica (Pitilla Field Station, 10°59' N, 85°26' W), French Guiana (Petit-Saut Field Station, 5°03' N, 53°02' W), and one distant site in Brazil, *i.e.*, Cardoso Island (Parque Estadual da Ilha do Cardoso, 25° 03' S, 47° 53' W). A description of the sampling sites was given in **(Farjalla *et al.* in prep**). At each site, we identified two types of understorey habitats. Bromeliads in the open habitat received direct sunlight almost all of the day. Bromeliads in the closed habitat were shaded most of the day by overhead vegetation. Habitat openness was assessed on the basis of incident radiation (%IR) calculated from hemispherical photographs taken with a 28 mm camera lens above the bromeliads (see **Leroy *et al.* 2009** for methodological details).

Sampling tank-bromeliads

Ten large bromeliads of similar size were sampled in each habitat at each site. Sites differed in their bromeliad species. There is no evidence of species-specific associations between bromeliads and invertebrate species, however, the complexity and shape of the leaf arrangement is likely to influence the trophic structure of the aquatic community **(Srivastava 2006, Céréghino *et al.* 2011)**. We therefore selected bromeliads with similar leaf displays, *i.e.*, species with crateriform, *Vriesea*-like rosettes. For each bromeliad, we recorded the plant species, number of green leaves holding water, plant width (the average of two orthogonal measurements), plant height (a measurement from the base of its leaves to the highest point on the plant), and the elevation above ground. The water volume held by a plant at the time of sampling was measured by sucking out the water contained in each leaf using 10ml micropipettes and a graduated cylinder. The maximum water volume of each plant was then measured by slowly filling the empty bromeliad with a known volume of water until it was full to overflowing. The plant was then dissected and its leaves were rinsed in a bucket, to collect the invertebrates that were not pipetted. Live invertebrates were brought to the laboratory, where they were sorted and identified. The various taxa were partitioned into five functional feeding groups (FFGs, *sensu* **Cummins 1974**) based on gut content analyses **(Dézerald *et al.* 2013)** and on the literature **(Merritt & Cummins 1996)**. Predators feed on other animals. Filter feeders sift fine particulates, including living microorganisms, from the column of water. Gatherers collect fine particulates of organic matter from the debris that accumulates in the leaf axils. Shredders feed on coarse particulate organic matter > 1000 µm in size. Scrapers scrape off and consume the organic layer of algae, microorganisms and dead organic matter attached on the surface of the leaf litter and other coarse detritus (twigs, fallen fruits, *etc*.). The distribution of the species/functional groups among regions and habitats are reported in Table 3.1.

Table 3.1 The presence/absence of the functional groups in the different sites/habitats. Functional groups were assigned based on the BWG database; C=Cardoso/Brazil, CR=Costa Rica, FG=French Guiana, "+" and "-" denote presence or absence in the open/closed habitats.

Functional groups	Taxa	C	CR	FG
Predator	Odonate	+/+	+/+	+/+
	Dytiscidae	+/-	-/+	-/+
	Hydrophilidae	+/-	-/-	-/-
	Tabanidae	+/+	+/-	+/+
	Corethrellidae	+/-	-/-	-/+
	Dolichopodidae	-/+	-/-	-/-
	Ceratopogonidae	-/-	-/-	-/-
	Hirudinea	-/+	-/+	-/-
	Cecidomyiidae	-/-	-/-	+/-
	Veliidae	-/-	-/-	+/+
	Chironomidae	-/-	-/+	-/-
Shredder	Tipulidae	+/+	+/+	+/+
	Calamoceratidae	-/+	-/-	-/-
Scraper	Scirtidae	+/+	+/+	-/+
	Limnocytheridae	-/-	-/-	+/+
Filterfeeder	Culicidae	+/+	+/+	+/+
	Chironomidae	-/+	-/+	+/+
Gatherer	Oligochaeta	-/-	+/+	+/+
	Syrphidae	-/+	-/+	+/-
	Psychodidae	-/+	+/-	-/+
	Ceratopogonidae	-/-	-/-	-/-
	Chironomidae	+/+	+/+	-/-

Aquatic invertebrates and isotopic analyses

For each individual bromeliad, we determined the four most abundant detritivores and the two most abundant predators. Samples of any given invertebrate taxa in a bromeliad consisted of several individuals, to reduce the effect of between-individual variation on isotopic values. All individuals were starved in rainwater water from 24 h to 48 h for gut clearance, rinsed with tap water, and then oven-dried at 65 °C for 72 h. Natural δ^{13}C and δ^{15}N values of invertebrates were determined using a Thermo Delta V isotope mass spectrometer (IMS) interfaced to a NC2500 elemental analyzer at the Univ. Davis Stable Isotope Facility, USA. Final δ^{13}C and δ^{15}N values were expressed as ‰ relative to international standards: PeeDee Belemnite for C and atmospheric nitrogen for N. Analytical errors were 0.11‰ for δ^{13}C and 0.13‰ for δ^{15}N based on internal lab standards (animal standard).

Data analyses

Stable isotopes could be highly variable in time and space **(Guzzo *et al.* 2011)**. Therefore, we opted for a baseline correction provided by **Schmidt et al. (2011)**, which consists in standardizing each taxon position (including detrital samples) in the bi-plot space relative to a food web centroid. For each tank-bromeliad, the food web centroid was calculated as the mean δ^{13}C and δ^{15}N of all taxa. Then, differences in δ^{13}C and δ^{15}N from the centroid were calculated for each taxon. Hereafter, we refer to these new coordinates as ‘‘relative δ^{13}C and relative δ^{15}N’’, and use this as a means of defining trophic niche characteristics.

The relative contribution of the various detritivores to the diet of predators was analyzed using the R-package *siar*. This mixing model allows incorporating uncertainty in the stable isotope composition of sources as well as in the trophic enrichment factors **(Parnell *et al.* 2010)**. Uncertainty is also incorporated in diet estimates, which SIAR provides as true posterior probability distributions. Stable isotope ratios were entered for each individual invertebrate, while food source values were entered as means with SDs for each potential source. Required model input data include stable isotope composition of diet sources and invertebrate tissues, as well as trophic enrichment factor (TEF) data on the isotopic separation between diet sources and consumers. TEF values for invertebrates were obtained from the literature (δ^{13}C: 1.0 ± 0.5‰; δ^{15}N: 2.5 ± 0.5‰; **Caut *et al.* 2009**). Stable isotope data of invertebrates were grouped by FFGs, habitats (open and closed), and sites (French Guiana, Costa Rica, and Cardoso). The use of FFGs rather than species in mixing models is justified by several reasons. First, we analysed data covering large spatial scales where the composition of the species pool differs between sites. FFGs are based on invertebrate morphological and behavioural adaptations to acquire their food, and are thus independent of taxonomy. Second the R-package *siar* is more efficient at establishing the diet of predators from a few distinct sources (4 FFGs) than from numerous sources represented by taxa *per se*.

A first step consisted in evaluating changes in the relative contribution of the different FFGs to the diet of predators in the various habitats across all sites we then further partitioned the relative influence of habitats and sites in the diet of each individual odonate. Since the percent contribution of one particular detritivore depends on the presence of other detritivores in the environment, we transformed the percentage matrix into a dissimilarity matrix using the Aitchinson transformation for proportional data (R-package *compositions*). Dissimilarity squared matrices display two-by-two comparisons giving the extent to which two predators are dissimilar based on their diet. We then performed a permutational analysis of variance (permANOVA) on the dissimilarity matrices of odonates as response variables and with "habitats" (categorical variable with 2 levels: open or closed), "sites" (categorical variable with 3 levels: French Guiana, Costa Rica or Cardoso) as explanatory variables. The distance-based permANOVA performed basic ordination of the dissimilarity matrix under the constraint of the environmental variables (R-package *vegan*). This procedure allowed us to assess the significance of environmental variables on odonates' diet. We used habitats and sites as proxy of changes in environmental conditions and in the composition of the species pool however these categorical variables hide substantial turnover in prey biomass. Therefore, we also evaluated how changes in prey biomasses were reflected in consumers' diet using Kendall's correlation coefficients. All statistical analyses in the present study were conducted using the R software V. 3.2.1 **(R Core Team 2015)** under a 95% confident interval.

RESULTS

Contribution of the functional groups to predators' diet

All functional groups were found at all regions and habitats and seem to contribute at least 1/4 of predators' diet, but patterns in trophic pathways were not consistent among study sites. This suggests that both local environments and regional species pools influenced the main trophic pathways within faunal food webs (Table 3.2, Figure 3.1). Macroinvertebrate FFGs that process coarse detritus (shredders and/or scrapers) however represented the higher proportion of diet sources in several habitats and countries. In particular, shredders likely contributed 27-45% to predators' diet (Table 3.2) except in open habitats of Costa Rica (Figure 3.1D) and closed habitats of Cardoso (Figure 3.1E). Among FFGs that rely on fine particulate organic matter, scrapers were also an important food source to predators (23-39%), except in open habitats of French Guiana (<20%). Finally, gatherers as food sources tend to be consistently overlooked by predators except in open habitats of French Guiana (18%).

Table 3.2 Mean contributions (±SD) of the various functional feeding groups to the diet of odonates in the different habitats (open or closed) and sites: French Guiana (FG), Costa Rica (CR), Cardoso (C; Brazil).

Sites	Habitats	Filter feeders	Gatherers	Shredders	Scrapers
FG	Open	0.20±0.13	0.18±0.13	0.45±0.16	0.17±0.12
	Closed	0.24±0.13	0.13±0.09	0.38±0.15	0.25±0.12
CR	Open	0.29±0.16	0.14±0.11	0.23±0.14	0.34±0.15
	Closed	0.22±0.14	0.20±0.13	0.35±0.12	0.23±0.13
C	Open	0.27±0.15	0.17±0.12	0.27±0.15	0.29±0.15
	Closed	0.19±0.13	0.18±0.13	0.24±0.15	0.39±0.18

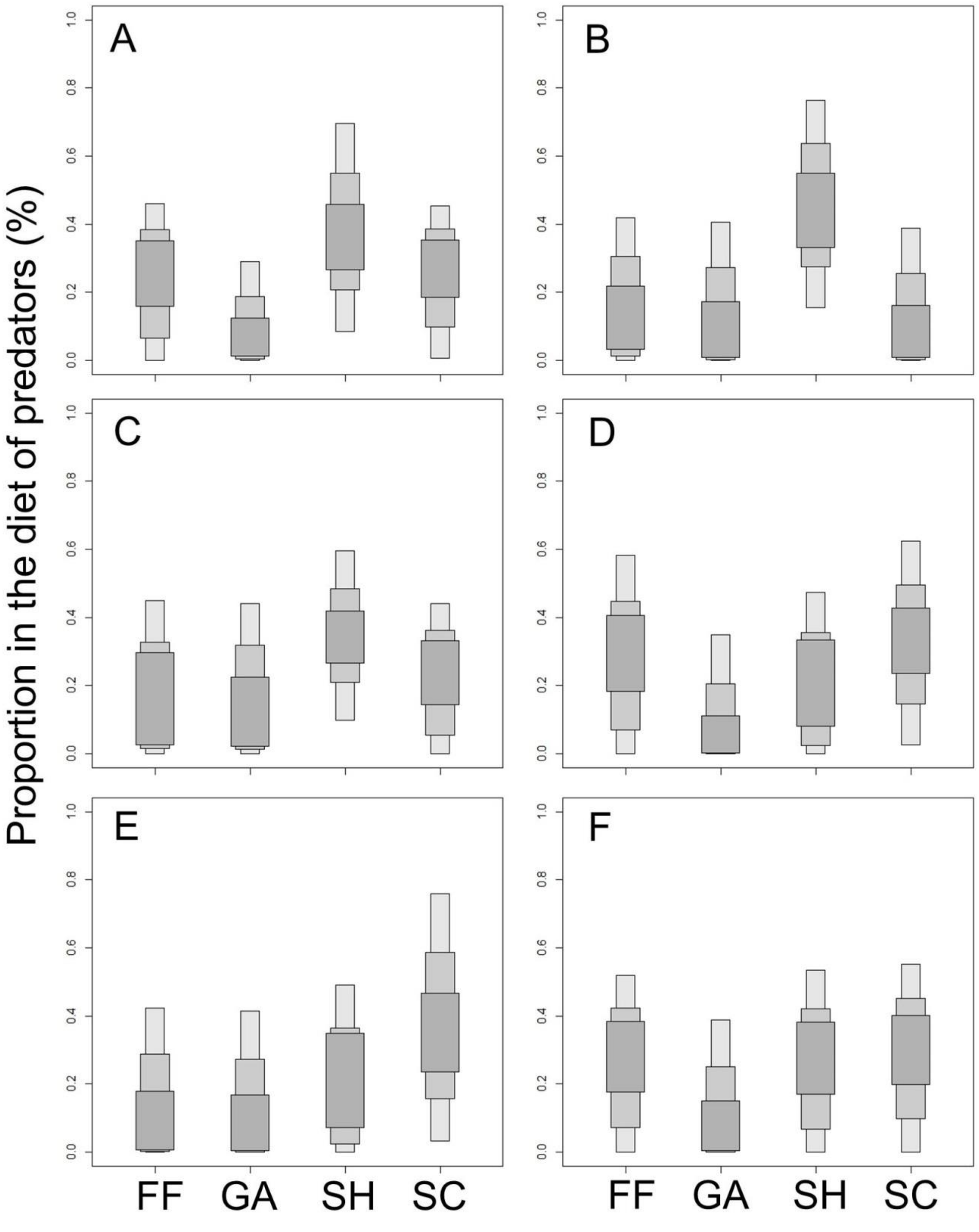

Figure 3.1 Percent contribution of each functional feeding group to the diet of odonates in closed (panels A, C, E) and open (panels B, D, F) habitats in A-B) French Guiana, C-D) Costa Rica, and E-F) Cardoso/Brazil. FF = filter feeders; GA = gatherers; SH = shredders; SC = scrapers. Boxes' color defines the credibility intervals: dark grey = 25%; grey = 50%; light grey = 95%.

The diagnostic of the posterior dietary proportions of odonates (Figure 3.2A-F) and credibility intervals in Figure 3.1A-F indicates that models were moderately efficient at discriminating the contribution of some sources to the diets of predators. Likely explanations are the high variability in isotopic signatures of the resources considered and/or the very voracious and generalist predatory behavior of odonate larvae in their resource use.

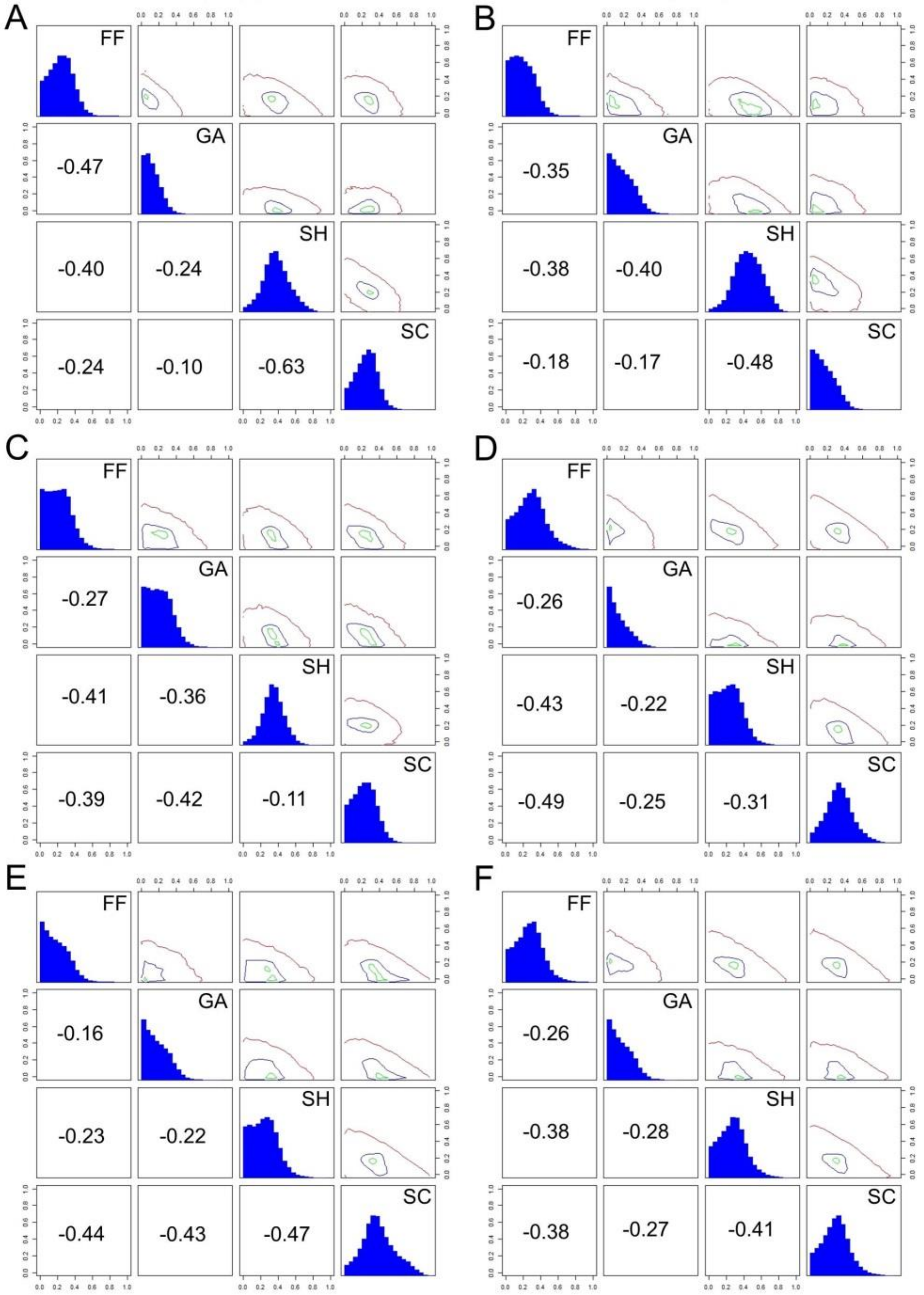

Figure 3.2 Matrix plot of the posterior dietary proportions of odonates. The upper-triangle shows a contour plot, the diagonal a histogram, and the lower-triangle the correlation between the different sources in closed (panels A, C, E) and open (panels B, D, F) habitats in A-B) French Guiana, C-D) Costa Rica, and E-F) Cardoso/Brazil. FF = filter feeders; GA = gatherers; SH = shredders; SC = scrapers. More negative correlation coefficients indicate that SIAR models had troubles differentiating the two sources.

Influence of habitats and sites on trophic pathways

Regardless of habitat type or site, odonate larvae were the most abundant predators (Table 3.1). We further partitioned the relative influence of “habitat” and “site” on the diet of odonates. Most of the variability in the diet sources of odonates was significantly explained by the interaction between habitats and site, (Table 3.3). For instance, odonate larvae rather fed on shredders in French Guiana (38%) and Cardoso (27%), whereas fed equally on all four FFGs in Costa Rica (35% each). In the models, the site:habitat interaction explained 6% of the total variance for odonates (p = 0.041).

Table 3.3 Influences of habitat and regions on trophic pathways. The effects of the different environmental variables and their interaction on the diet of odonates were tested using an analysis of variance with permutations. “Sites” includes French Guiana, Costa Rica and Cardoso/Brazil; “Habitat” is either closed or open areas within each site.

Models	Variable	Df	Sums of squares	F	R2	P-value
Odonates	Habitat	1	0.92	2.95	0.03	0.038
	Sites	2	1.99	3.19	0.07	0.012
	Sites*Habitat	2	1.65	2.65	0.06	0.041
	Residuals	72	22.42		0.83	
	Total	77	26.97		1.0	

Overall, the environmental variables explained 17% of the total variance in predators’ diet. This high variability in predator’s diet is reflected in the isotopic niche envelops of the different functional feeding groups in the relative isotopic biplot space (Figure 3.3). Isotopic niche envelops show inconsistent patterns across sites and habitats. For instance, gatherers and scrapers in open habitat of French Guiana have large and small envelop surfaces, respectively, whereas closed habitats of Cardoso display the reverse pattern.

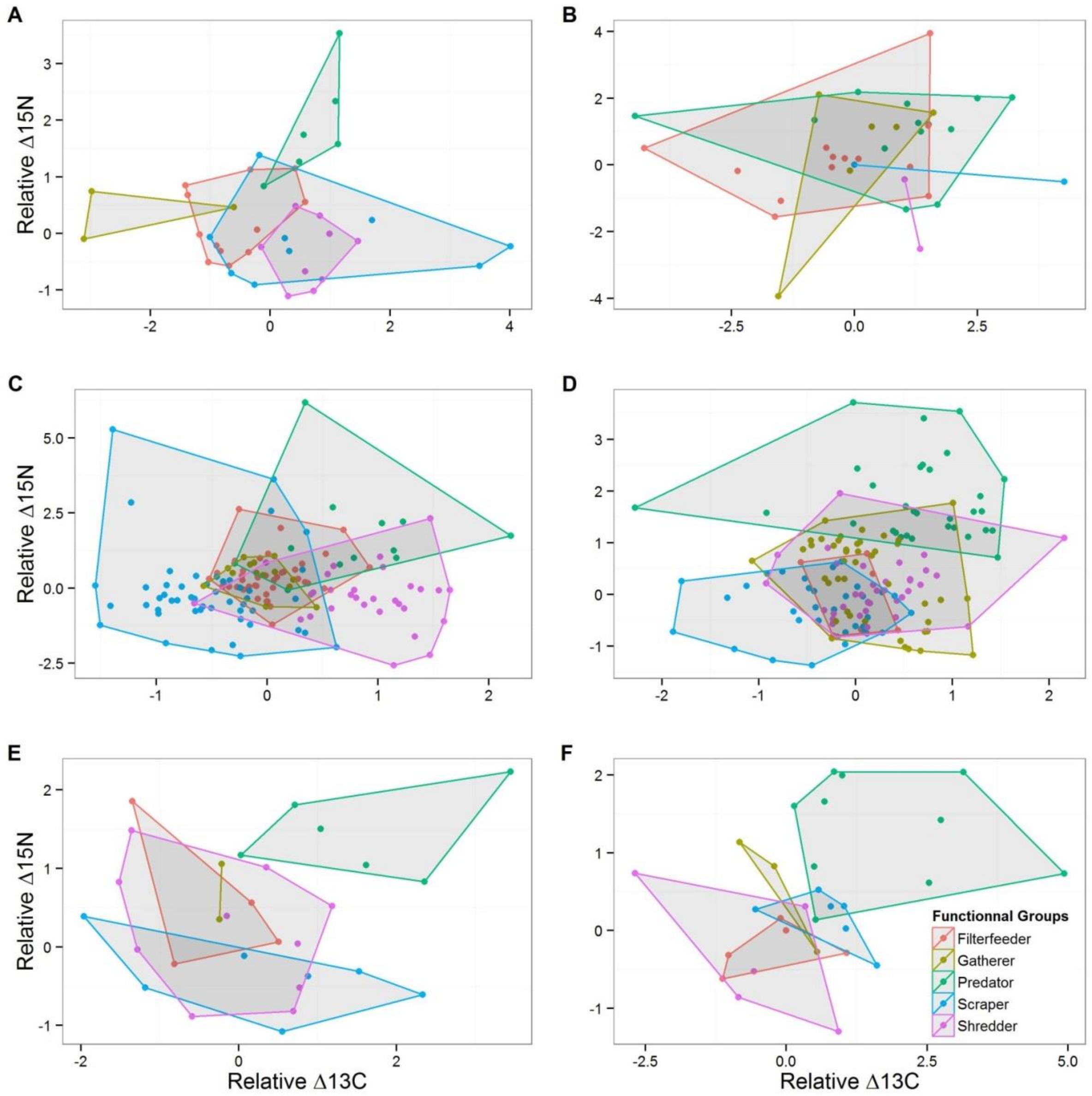

Figure 3.3 Isotopic niche envelops of the different functional feeding groups in the relative isotopic biplot space in closed (panels A, C, E) and open (panels B, D, F) habitats in A-B) French Guiana, C-D) Costa Rica, and E-F) Cardoso/Brazil. Note that axis scales vary among panels.

Influence of prey relative biomasses on trophic pathways

Regardless of study sites and habitats the mean contribution of the different functional feeding groups to predators' diet was not significantly correlated with the biomass of prey species within tank bromeliads (Kendall's coefficient = 171, p = 0.107). Within each site, this correlation was positive and significant in Costa Rica (Kendall's coefficient = 23, p = 0.03, Tau = 0.64) but not significant in the remaining sites (French Guiana and Cardoso, Kendall's coefficient = 19 and 12, respectively; p = 0.275 and 0.72, respectively; Figure 3.4).

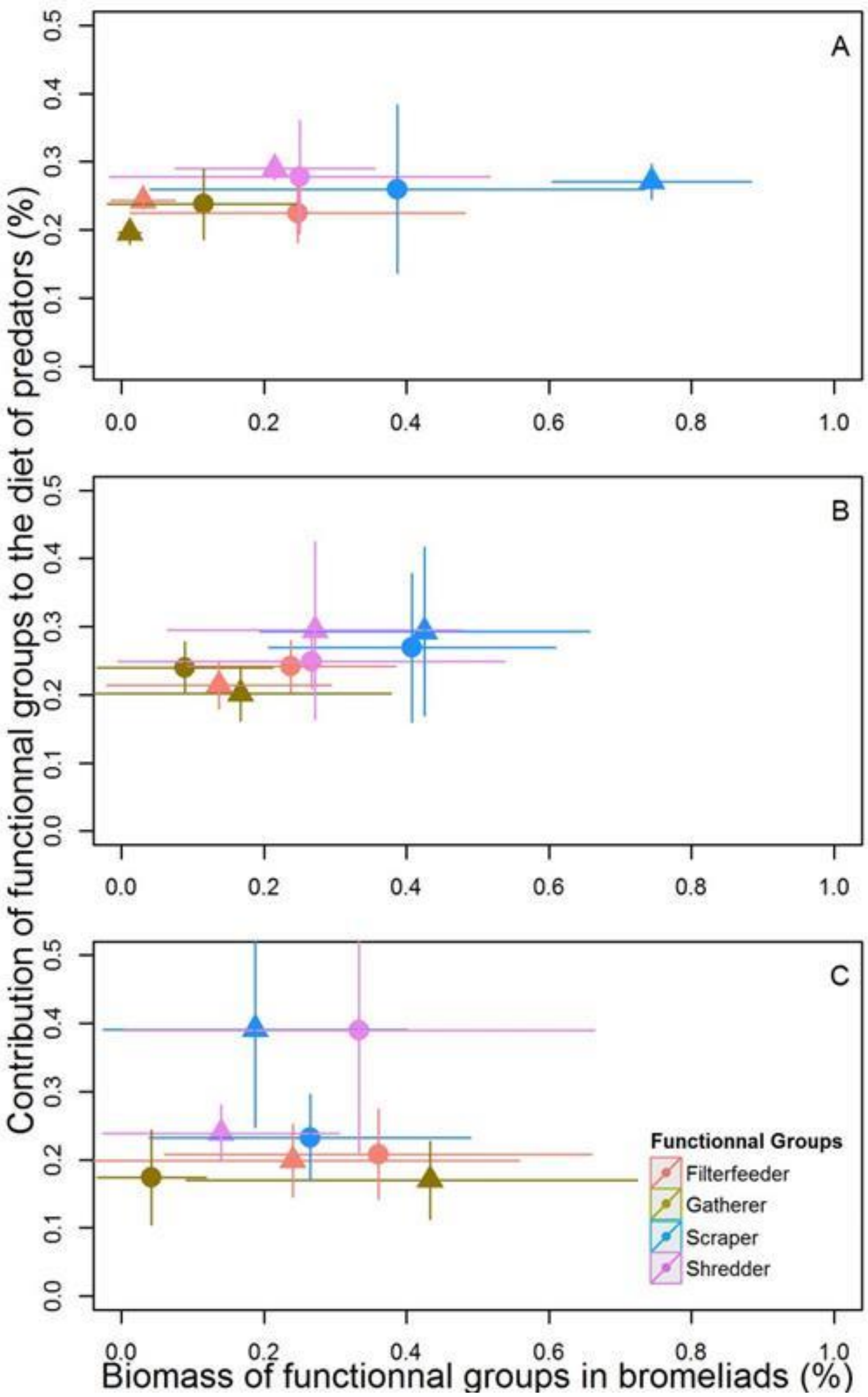

Figure 3.4 Mean percent contribution (±SD) of the different functional feeding groups to the diet of odonates as a function of their relative biomass within the community in closed (circles) and open (triangles) habitats. A) French Guiana; B) Costa Rica; C) Cardoso/Brazil. Relationships between variables were only significantly correlated in Costa Rica (Kendall's correlation coefficients = 0.64, P = 0.03).

DISCUSSION

Tropical rainforests form naturally heterogeneous and complex ecosystems from local to continental scales. Our approach uses data from more than 60 distinct replicates across a latitudinal gradient and allows inferring consistencies and site-specific features in the way energy and matter flow through food chains. All functional feeding groups were found along this spatial gradient ensuring main ecosystem functions. Despite substantial variability in trophic pathways due to prey species turnover and differential predatory behaviors from site-to-site, some trends in the top-down control of certain functional groups were consistently detected (*e.g.,* shredders seem preferentially consumed and gatherers neglected). We further discuss the use of stable isotopes for mixing models in bromeliads and the influence of habitats and sites on trophic pathways and the implications for ecosystem functioning.

Consistency in trophic pathways across spatial scales

The predatory larvae of odonates were found throughout the latitudinal gradient, *i.e.,* from Costa Rica, French Guiana, to Cardoso (Brazil). The ubiquitous odonate larvae represent a substantial fraction of the aquatic community as found by others **(Petermann *et al.* 2015)** and seemed to have sampled almost equally all available functional groups within tank bromeliads suggesting that this system is strongly driven by top-down processes **(Ngai & Srivastava 2006)**. Nonetheless, shredders tend to be preferentially consumed contrary to gatherers, which are consistently avoided across study sites. Indeed, Chironomidae and Naididae are the main taxa within the gatherer functional groups and rely upon a mixture of fine organic matter that sediment at the base of bromeliad leaf axils. These organisms thus forage within the fine and coarse material. This spatial position within the water column is likely to represent a micro-refuge from predation pressure. Likewise, some filter feeders, Culicidae in particular, are capable of mitigating the effect of top predators via behavioral adaptions in predator avoidance **(Hammill *et al.* 2015)**. This observation may partly explain the moderate impact of odonate larvae on the filter feeder functional group.

Shifts from closed to open habitats induced some changes in trophic pathways, but these modifications were not consistent among sites suggesting that spatial turnover in species composition and biotic interactions could interact with the habitats. For instance, communities in Costa Rica face a shift from the numerical dominance of Calamoceratidae in open habitats to a system dominated by Tipulidae in closed canopy areas. The former taxon is tightly encapsulated in a solid sheath preventing their consumption by predatory larvae and resulting in a habitat-induced shift in predators' diet (personal observations). In addition, open habitats have been found to further influence trophic pathways via a qualitative modification of the resource at the base of bromeliad food webs. Sun-exposed tank bromeliads support both detritus- and algal-based food webs **(Farjalla *et al.* in prep, Marino *et al.* 2011, Brouard *et al.* 2012)**. Autotrophic production could provide a complementary and nutrient-rich source to aquatic invertebrates. These qualitative changes between habitats come along with a potential increase in resource quantity in open compared to closed habitats as tank bromeliads accumulated more water in the former area. These differences between bromeliads from open and closed habitat were especially strong at the Brazilian site.

The sites and habitats may influence trophic pathways through changes in the specific composition/relative biomass of predator and/or prey assemblages. If a given predator is generalist in its resource use, the numerical and biomass dominance of a given prey item, here, filter feeders, gatherers, shredders and/or scrapers, should lead to a greater contribution to the diet of this predators as specified by the neutral interaction assumptions **(Yeakel *et al.* 2011)**. Otherwise, predators would rather display a behavioral preference for a given prey, regardless of the prey relative biomass. Contrary to our expectations predatory larvae significantly tracked shifts in prey biomass in only one study site (Costa Rica). One could then argue that odonates are, to some extent, relatively specialized in their resource use. The variability in isotopic niches of predators offers a counterargument to this assumption. In fact, our results indicate that individual predatory larvae could be specialized on a given prey item but it would only reflect prey availability at that moment. Finally, the sum of all individual diets would result in a wide diet range at the species level, a typically observation for generalist species **(Bolnick *et al.* 2003)**. Altogether, these results suggest that local environmental processes (biotic interactions) are likely to be as important as broad-scale biogeography in determining trophic pathways **(Jardine 2014)**.

Confidence in estimations of predators' diet

The isotopic signature of consumers' tissues was believed to directly represent their diets. This previous assumption was challenged as consumers could have a given isotopic signature and contrasting diet preferences if various sources have similar isotopic niches. In contrast, a consumer species in different habitats could consume the same resource with more or less variability in stable isotopes **(Bolnick *et al.* 2003, Quevedo *et al.* 2009, Schmidt *et al.* 2011)**. The assessment of the performances of mixing models provided moderate confidence at discriminating the contribution of some sources to the diets of predators. A likely explanation is the high variability in isotopic signatures of all functional feeding groups including the predatory larvae (Figure 3.3).

As suggested by **Semmens *et al.* (2009)**, some caveats must remain in mind when trying to infer consumers' diet from stable isotopes. First, all prey sources should be sampled, identified, and their isotopic signatures properly quantified in time and space. In this sense, the protocol in this study provided some confidence in our isotopic data by using all tissues of a given individual and several individuals per species within more than 60 bromeliads (replicates) across South America. Second, the isotopic signature of prey sources should be sufficiently distinct to provide accurate estimates of resource partitioning. Bromeliads are mainly detritus-based ecosystems, where almost "everything eats everything". This observation can be seen as a limitation of our analyses or it may be a general feature of bromeliad ecosystems.

Third, antagonistic interactions within or among trophic levels, *i.e.*, intraguild predation and/or omnivory could induce some noise in mixing models, especially in large-bodied and voracious consumers such as odonate larvae. For instance, some studies in European streams have found that a large amount of decomposing material (up to 54%) was actively ingested by consumers at the apex of food chains **(Fenoglio *et al.* 2007, Frauendorf *et al.* 2013)**. An ontogenetic diet shift could also occur from detritus-driven diets in early instars to consumption habits dominated by live organisms in late predatory instars **(Céréghino 2006)**. Although odonate may not purposely feed upon detritus as they are attracted by prey movements and use sit-and-wait predation techniques, these predators could inadvertently ingest detritus by swallowing prey individual as a whole. The effects of intraguild predation have not been evaluated in this study but we suggest that investigating the prevalence of such interactions in a system controlled by top-down processes could have broad implications for ecosystem functioning. Finally, the extent to which, isotopic fractionations are correctly quantified and are invariant across habitats and/or sites within species, is the last caveat highlighted by **Semmens *et al.* (2009)**, but unknown in this study.

Concluding remarks

All functional feeding groups were consistently found throughout the latitudinal gradient thus maintaining the principal ecosystem functions. Taxonomic diversity has been recently found to positively influence ecosystem functionality across aquatic and terrestrial habitats **(Lefcheck *et al.* 2015)**. These recent results raise the question of the importance of species redundancy within functional feeding groups in bromeliad ecosystems? The impact of a predator on a given ecosystem function would be different if it prey upon a species-rich or a depauperate functional group. In particular, decomposition is a key regulator of global carbon and nutrient dynamics **(Cebrian & Duarte 1995, Srivastava *et al.* 2009)** and seems to be strongly controlled by top predators in bromeliad ecosystems **(Ngai & Srivastava 2006, Srivastava & Bell 2009)**. Future research should further investigate the far reaching consequences of top-down processes on the structure of multitrophic networks and their resulting functioning.

To some extent, trophic pathways are predictable across broad biogeographic scales as large-bodied and generalist predators will sample almost equally all species within functional feeding groups given that the corresponding prey items do not reach a prey-size refuge or acquire predator-avoidance traits. However, the strength of top-down control on these prey depends substantially upon the turnover in prey assemblages from the regional pool. This study suggests that global changes by disproportionately affecting large bodied predators may have critical impacts on decomposition processes and nutrient cycling through indirect interactions and strong top-down processes. Additionally, local environmental factors such as species interactions and micro-environmental conditions are likely to be as important as broad-scale biogeography and climate in driving food-web patterns. Investigating how fluxes of energy and matter, vary across spatial and temporal scales, may help unravel broad scale-independent mechanisms of ecosystem functioning.

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PARTIE II

Chapitre 4: Temperature:diet interactions affect survival through foraging behavior in a bromeliad-dwelling predator

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Abstract. Temperature and food quantity and quality play important roles in insect growth and survival, influencing population dynamics as well as interactions with other community members. However, the interaction between temperature and diet and its ecological consequences have been poorly documented. *Toxorhynchites* are well-known biocontrol agents for container-inhabiting mosquito larvae. We found that *Toxorhynchites haemorrhoidalis* larvae (Diptera: Culicidae) inhabiting water-filled rosettes of tank bromeliads catch and eat prey of both aquatic (mosquito larvae) and terrestrial origin (ants), using distinct predatory methods. They carried out frontal attacks on ants, but ambushed mosquito larvae. In choice tests, *T. haemorrhoidalis* favored terrestrial prey. Temperature had a significant effect on predator development and survival through its interaction with diet, but did not alter the preference for ants. *T. haemorrhoidalis* larvae emerged quickly when fed only mosquito larvae, whereas all individuals died before pupation when fed only ants. We conclude that behavioral factors (*i.e.*, attraction to ants that disturb the surface of the water) overtake physiological factors (*i.e.*, the adverse outcome of elevated temperature and an ant-based diet) in determining a predator's response to temperature:diet interactions. Finally, because *T. haemorrhoidalis* larvae preferentially feed on terrestrial insects in tank bromeliads, mosquito larvae may indirectly benefit from predation release.

Key words: biocontrol agent; development; French Guiana; selective feeding behavior; tank-bromeliad; Toxorhynchites haemorrhoidalis

INTRODUCTION

Ecological communities form complex networks, among which food webs are the most studied. Most predatory species are thought to modify their linkage patterns with other species following changes in relative density or biomass **(Kondoh 2003)**. Foraging theories postulate that a consumer species selectively feeds upon species that provide it the highest net energy intake per unit effort **(Emlen 1966, MacArthur & Pianka 1966)** and that if preferred prey become less available, the predators can consume less energetically suitable prey **(Emlen 1966, MacArthur & Pianka 1966, Thierry *et al.* 2011)**. Such behavioral flexibility would be crucial for development and survival when facing environmental fluctuations (*e.g.,* in temperature, quality and availability of food). Nonetheless, observations demonstrating the prevalence of this flexible behavior in nature are needed to validate these assumptions **(Kondoh 2003, Acheampong *et al.* 2014, Dell *et al.* 2014)**.

Temperature and food quantity and quality have major effects on insect growth and survival. Temperature affects the metabolic rates of ectotherms such as insects, strongly governing development patterns, survival, reproduction, and many other aspects of population dynamics **(Visser & Both 2005, Logan *et al.* 2006, Régnière *et al.* 2012)**. Hence, physiological constraints and metabolic demands should rise with global warming, pervasively altering the functioning of entire communities **(Petchey *et al.* 1999, Brown *et al.* 2004, Petchey *et al.* 2010, Woodward *et al.* 2010a, Yvon-Durocher *et al.* 2011)**. When not living in microsites that buffer exposure to environmental changes, mobile insects use sensory tools (*e.g.,* antennae) to detect thermal fluctuations and move to thermally optimal habitats. Compared with physiological traits, behavioral traits may allow for more ecological flexibility towards thermal fluctuations by triggering faster responses (*e.g.,* avoidance, mitigation) to unsuitable conditions.

The resources used by insects vary widely in quality (nutritional value) and availability (*e.g.,* density, biomass and/or distribution in space and time). Insects can quickly respond to sub-optimal food conditions by preferentially selecting food of high nutritional quality or by increasing intake rates **(Mitra & Flynn 2005)**. Sub-optimal food conditions are particularly stressful for insects that must store sufficient resources during larval feeding stages to support the development, dispersal and reproduction of adults, non-feeding adults in particular. The effects of temperature or food fluctuations on individual physiology and behavior are well-studied in herbivorous species **(Behmer 2009)**. However, there have been few attempts to disentangle such effects in predaceous insects (but see **Traniello *et al.* 1984**).

Toxorhynchites culicids are well-known biocontrol agents against container-inhabiting mosquito larvae, although their effectiveness has been questioned because their biology and behavior are insufficiently characterized **(Collins & Blackwell 2000, Focks 2007)**. Some predatory larvae of *Toxorhynchites* sp. inhabiting the water-filled rosettes of tank bromeliads (Bromeliaceae) forage at the water-air interface, where they prey on aquatic and terrestrial invertebrates (mosquito larvae and ants, respectively) throughout their larval life span **(Linley 1995, Campos & Lounibos 2000)**. For instance, *T. haemorrhoidalis* (Fabricius) is common in bromeliad axils as well as *Heliconia* flower bracts in northern South America **(Lounibos *et al.* 1987)**. Owing to their small catchment and high terrestrial:aquatic surface ratio, bromeliad pools contain suitable model organisms to assess if temperature-induced changes in metabolic demands alter predatory behavior as well as aquatic *vs*. terrestrial prey selection in top predators. Assuming that (1) the metabolic demands of individuals increase with increasing temperature **(Trpis 1972)**, and (2) *T. haemorrhoidalis* selectively feeds on the species (*i.e.*, either mosquito larvae or ants) that provides the highest energy intake under ambient conditions, we tested the hypothesis that the preference for a prey species would remain unchanged with experimental warming, despite an increase in prey consumption.

MATERIAL AND METHODS

Study species and sample collection

In French Guiana, the larvae of *T. haemorrhoidalis* are among the largest and most numerically dominant predators (including odonate and tabanid larvae) in the aquatic communities dwelling in tank-bromeliads. These larvae grow through four instars and are considered generalist predators that can exhibit cannibalistic behavior. To test how temperature-diet interactions affect *T. haemorrhoidalis* survival, we conducted experiments in the laboratory in Kourou, French Guiana, from March to July 2013. We sampled all of the aquatic insects (*i.e.*, *T. haemorrhoidalis* and other Culicidae larvae) from two tank bromeliad species. We sampled *Aechmea mertensii* Schult.f. (Bromeliaceae), which obligatorily grows on ant gardens (AGs; **Benzing 2000**) inhabited by either the ants *Camponotus femoratus* Fabr. (Formicinae) or *Neoponera goeldii* Forel (Ponerinae) near the Petit-Saut dam (05°03′30.0″N;

52°58′34.6″W). We sampled *Aechmea aquilega* Griseb. (Bromeliaceae) near the city of Sinnamary (05°22′42.9″N; 52°57′11.9″W). Contrary to *A. mertensii*, *A. aquilega* is facultatively associated with ants, which build their nests within the leaf rosette. To collect aquatic invertebrates from the tanks, we carefully emptied the wells in each plant by sucking out the water using 10-ml and 50-ml pipettes with the end trimmed to widen the orifice **(Jabiol *et al.* 2009, Jocqué *et al.* 2010)**. We pooled all of the invertebrate samples regardless of origin.

Gut contents

We used gut contents to quantify the relative importance of the various prey items. After collection in the field, we preserved 30 third/fourth instar larvae in formalin (4%) for subsequent dissection (*N* = 17 from *A. mertensii* and *N* = 13 from *A. aquilega*). We collected late instar larvae because, within invertebrate food webs, the largest individuals within a species have the greatest effect on energy flows **(Céréghino 2006)**. We determined the diet of *T. haemorrhoidalis* larvae by dissecting the entire gut, and analyzing it with a microscope (Optiphot-2 Nikon®). Most prey items could be identified and enumerated by comparing chitinous fragments (*e.g.,* head capsules or the legs of insects and the setae of Oligochaeta) with specimens of tank-bromeliad invertebrates archived in our collection (University of Toulouse 3, France.).

Resource preference and predation behavior

Examination of the gut contents suggested that ants constituted a substantial fraction of *T. haemorrhoidalis'* diet, but mosquito larvae are the most abundant prey species at our study site **(Dézerald *et al.* 2014)**. Therefore, we conducted two-way choice tests on 30 third and fourth instar *T. haemorrhoidalis* larvae (*N* = 9 from *A. mertensii* and *N* = 21 from *A. aquilega*; body size = 8.29 ± 0.11, *N* = 30) by offering them *C. levior* ants (taken from AGs; body size = 1.72 ± 0.03, *N* = 30) and *Wyeomyia pertinans* mosquito larvae (body size = 3.91 ± 0.17, *N* = 30). We placed *T. haemorrhoidalis* larvae into separate plastic tubes (diameter = 3 cm; height = 7 cm; water volume = 40 ml) behind a rigid plastic strip (width = 3 cm; length = 8 cm) at ambient temperature (water temperature = 25 ± 0.5°C). On the other side of this strip, we placed one mosquito larva in the water column and one ant on the surface of the water. The plastic strips prevented premature attacks while adding the prey. After ten seconds, we pulled the strip out of each tube and recorded the predator's vertical position in the water column, which prey species was attacked first, total number of attacks per prey item, and which prey was consumed. After a deadly attack, the other prey was removed. If no attack occurred after 15 minutes, we removed both prey. Finally, we repeated the two-way choice tests for each individual predator at three-day intervals. We did not feed the larvae between the two tests.

A total of 90 tests (30 tested individuals across three successive tests) were validated. Before testing for a potential prey preference, we verified if *T. haemorrhoidalis* individuals displayed learning in their predatory behavior. We used an extension of generalized linear models (GLMs), generalized estimation equations (GEEs), because GEEs accommodate repeated observations on the same individual **(Liang & Zeger 1986)**. In GEEs, an association structure between subsequent observations or measures from the same individual must be specified. We recorded behavioral observations every three days (time-ordered dataset), so we selected an auto-regressive correlation structure **(Zuur *et al.* 2009)**. We tested the null hypothesis that the number of attacks towards ants and mosquito larvae in the three successive tests are the same. Conversely, if attacks increased or decreased across successive tests it would suggest learning had occurred. In these models, the response variables were the species of prey that was first attacked, the total number of attacks directed towards ants or mosquitoes, and the prey species that overcame deadly attacks. For each response variable, two separate models were used for ants and mosquitoes. The three successive tests were entered as a categorical (three levels) explanatory variable. Finally, we carried out proportion tests with Yates' continuity correction for one sample on the total number of first attacks, the total number of attacks, and the total number of deadly attacks directed towards ants and mosquitoes. We conducted these proportion tests on either all or each successive test separately depending on the GEE results. The latter analyses allowed us to assess if predatory larvae preferred either ants or mosquitoes, while taking potential learning into account.

Effect of temperature and diet on prey consumption and development

We collected 63 first instar *T. haemorrhoidalis* from the field (*N* = 11 from *A. mertensii* and *N* = 52 from *A. aquilega*) and placed them into separate plastic tubes (diameter = 3 cm; height = 7 cm) in the laboratory at an ambient temperature (25 ± 0.5°C). We fed them with mosquito larvae (*W. pertinans*) until they reached third instar. Then we randomly conditioned the larvae at three different water temperatures. We selected experimental temperature according to a pilot study where we placed small data loggers (iButtons$^{©}$; Maxim Corporation, Dallas, TX) in the central reservoir of two bromeliads located in forested and open areas for two weeks during the dry season, monitoring temperatures every hour. Temperatures oscillated between 22°C and 33°C with a mean of 24.6 ± 0.06°C and 28.3 ± 0.08°C (± SE, *N* = 425) in the forested and open areas, respectively. Therefore, we placed tubes in large plastic trays filled with water at 25 ± 0.5°C, 29 ± 0.5°C and 33 ± 0.5°C (21 tubes per tray, one *T. haemorrhoidalis* per tube). We set the water temperature in the trays using 50-watt electric immersion heaters for aquariums (Visitherm Eco®, http://www.aquariumsystems.eu/).

Finally, we provided different food items to fourth instar larvae (summarized in Figure 4.1). For each temperature treatment, we fed seven larvae *ad libitum* with either mosquito larvae or ants, and provided the remaining seven individuals with ants and mosquito larvae in equal proportions. In the latter treatment, if the *T. haemorrhoidalis* ate all of the mosquito larvae or ants, we added more individuals from both taxa. To prevent the ants from escaping and for the sake of consistency among treatments, we put the tube caps on top of all tubes (unscrewed) although the ants were rarely able to leave the water surface and climb the tube walls. We recorded elements of the predator's development every three days for the rest of their aquatic cycle, namely: days spent in the trays, if the larvae pupated or died, number and type of prey consumed, and mean consumption rate. We calculated the latter variable as the number of prey available for predatory larvae minus the number of live prey in the tubes after three days, divided by the total number of days spent in the trays. Since prey occasionally died due to unknown causes (no apparent signs of 'wasteful' killing behavior by predatory larvae), we replaced both eaten and dead prey. At the end of the experiment, we collected the *T. haemorrhoidalis* pupae, and oven dried them at 60°C for 48 h to obtain dry mass.

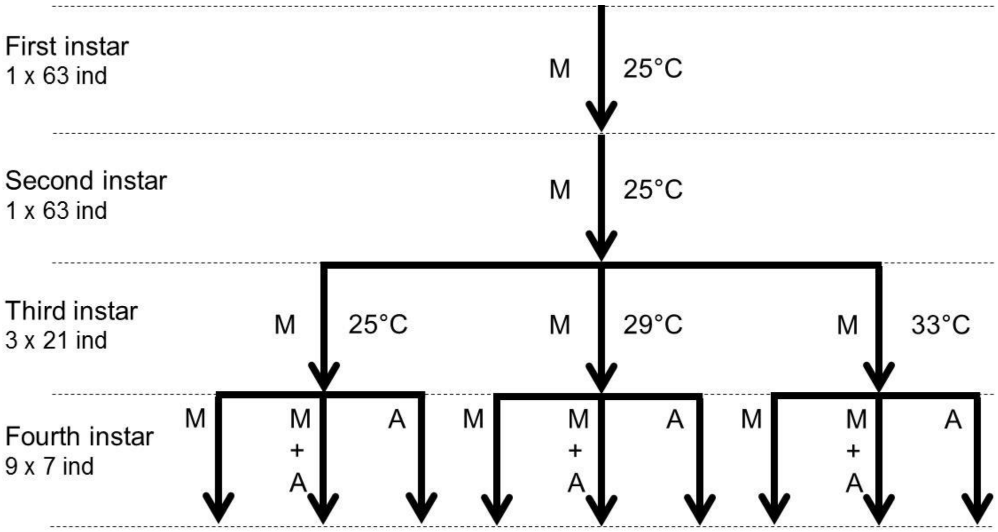

Figure 4.1 Schematic representation of the experimental design of the temperature:diet interactions. On the left is the number of Toxorhynchites haemorrhoidalis *individuals within each larval stage (from one to four instars) according to the different temperature and food treatments.* T. haemorrhoidalis *larvae were provided with either mosquito larvae (i.e.,* Wyeomyia *sp.), ants (*Crematogaster levior*) or both (M, A, M+A) in three temperature treatments (25°C, 29°C, and 33°C).*

Data analysis

To determine the overall effect of diet and temperature on *T. haemorrhoidalis,* we used GLMs with the time needed to reach the final state (*i.e.,* dead or pupa), and the final state as response variables. Because the time spent in trays could partially confound negative or positive effect on survival, we utilized two distinct models, *i.e.*, one model for development time, and one for final state. The explanatory variables were diet, temperature, and their interactions (two factorial variables with three levels). Since the time needed to pupate is expressed in days (count-based data) and the final state is a binomial variable, we fit the models with Poisson and binomial families. We conducted an Akaike Information Criterions (AIC)-based selection on the GLMs and graphically assessed the validation of the final models. To test the hypothesis that increasing temperature positively affects consumption rates, we conducted a Kruskal-Wallis test with the mean consumption rates of mosquito larvae or ants as entered variables and temperatures as explanatory variables. To further evaluate the effects of both diet and temperature on predator development, we assessed changes in consumption habits over time. For each *T. haemorrhoidalis* larva, we regressed the number of prey consumed every three days against time. We used GEEs with an auto-regressive correlation structure as described for the choice tests. Moreover, for *T. haemorrhoidalis* raised with both mosquitoes and ants, we used two separate models. We assessed the temperature effect on slope estimates within a given diet treatment using a Kruskal-Wallis test. We compared the consumption of either mosquitoes or ants when the larvae were provided with either one or both prey species using a Wilcoxon Rank Sum test. We evaluated all statistical analyses at 95% CI using R V. 3.2.1 **(R Core Team 2015)** with the add-on Geepack v. 1.1-6 package for GEE analysis (http://cran.r-project.org/doc/packages). We graphically assessed model validation (GLMs, and GEEs), evaluated the normality of residuals using Shapiro tests, and performed additional chi-square tests on the deviance and residual degrees of freedom for goodness-of-fit of the models (GLMs). We present the results as means ± SE throughout.

RESULTS

Gut contents

Overall, 20 of the 30 dissected *T. haemorrhoidalis* had identifiable prey fragments in their gut. Ants contributed on average 46.7 ± 0.12 percent of the diet. Other frequent prey were *Wyeomyia* spp. (Culicidae; 13.3 ± 0.07 % of the prey items) and Tanypodinae larvae (Chironomidae; 13.3 ± 0.1 %). Less frequent prey were *Tanytarsus* (Chironomidae), *Bezzia* sp., and Forcipomyiinae (Ceratopogonidae) (6.7 ± 0.07 % each), as well as *Culex* spp. (Culicidae 3.3 ± 0.03 %) and *Telmatoscopus* sp. (Psychodidae 3.3 ± 0.03 %).

Resource preference and predation behavior

T. haemorrhoidalis larvae spend most of their time resting and breathing at the water-air interface. A gentle tap on their plastic tube makes them swim downwards. Doing so after the strips were removed positioned the predatory larvae at the bottom of their tubes. The mosquito larvae behaved similarly when on the surface of the water, whereas the ants moved frantically on the surface of the water trying to reach the tube walls. *T. haemorrhoidalis* larvae responded quickly to the presence of ants by swimming towards them in a series of undulating backward movements. They then angled themselves at about 45° to the water's surface, and progressively adjusted their lateral position to face the ants. Once within striking distance, the predatory larvae curled up, swam vertically, seized the ants in their mandibles, and drowned them. Due to the ants' frantic movements and the air bubbles trapped by the ant setae that made them float, the predators struggled to maintain their position in the water column while breathing through their siphons. By contrast, when preying on mosquito larvae, *T. haemorrhoidalis* larvae acted as ambush predators. The predatory larvae remained motionless at the bottom of the tubes until the mosquito larvae swam close by. Then, they launched a lateral strike, grasped their aquatic prey, and swallowed the mosquito larvae within a few minutes.

The number of first attacks directed towards ants or mosquito larvae did not differ significantly across the three successive choice tests according to the GEEs (Table 4.1; ants: Wald = 0.07, $P = 0.79$; mosquito larvae: Wald = 0.8, $P = 0.371$). Overall, ants and mosquito larvae overcame 53 and 23 first attacks, respectively, and the proportion test indicates that *T. haemorrhoidalis* larvae were significantly more attracted by ants than by mosquito larvae (Figure 4.2A; Pearson $\chi^2 = 11.1$, $P = 0.0009$). However, whereas ants suffered a significantly higher total number of attacks for the first choice test compared to mosquito larvae (Pearson $\chi^2 = 60.1$, $P < 0.0001$), this number decreased significantly upon the third test (Table 4.1; Wald = 4.76, $P = 0.029$). For the third test, the total number of attacks did not differ significantly between the ants and mosquito larvae (Figure 4.2B; Pearson $\chi^2 = 0.78$, $P = 0.377$). These results indicate that the predatory larvae did not favor or reject a given prey after being presented with the other prey in earlier events, but *T. haemorrhoidalis* was more effective at capturing ants during the third test compared to the first one.

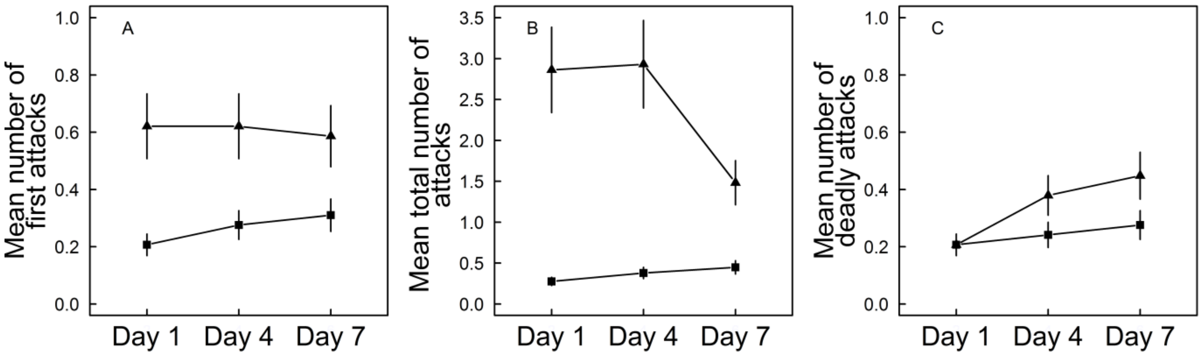

Figure 4.2 Distribution of attacks in three successive trials by 30 Toxorhynchites haemorrhoidalis *larvae leading to the consumption of ants (triangles) or mosquito larvae (squares) in two-way choice tests. The mean number of primary attacks (A), the mean total number of attacks (B), and the mean number of deadly attacks (C) are shown (error bars = SE). One test per* T. haemorrhoidalis *larva was run at three-day intervals for a total of the three events.*

Finally, *T. haemorrhoidalis* did not significantly increase the number of deadly attacks toward ants compared to those directed toward mosquito larvae (Table 4.1; ants: Wald = 3.69, *P* = 0.055; mosquito larvae: Wald = 0.37, *P* = 0.54). However, in all choice tests the numbers of deadly attacks were significantly higher toward ants than mosquitoes (Pearson χ^2, $\chi^2 = 7.9$, *P* = 0.005). Together, these results suggest that *T. haemorrhoidalis* larvae were significantly more attracted by ants at first sight, that over time they learned to better manipulate ants, and that the number of deadly attacks was significantly higher for ants than mosquitoes.

Table 4.1 Results of the generalized estimation equations (GEEs). Models were generated for three response variables: the prey species that was first attacked, the total number of attacks and the prey species that overcame the deadly attack. The prey were either mosquito larvae or ants.

Response variable	Models	Estimate ± SE	Wald	*P*
First attack	Ants			
	Intercept	0.49 ± 0.38	1.66	<0.0001
	Second test	4.72e-16 ± 0.54	0.00	1.00
	Third test	-0.01 ± 0.54	0.07	0.79
	Mosquitoes			
	Intercept	-1.34 ± 0.46	8.59	0.003
	Second test	0.38 ± 0.62	0.37	0.541
	Third test	0.55 ± 0.61	0.8	0.371
Number of attacks	Ants			
	Intercept	1.05 ± 0.21	25.27	<0.0001
	Second test	0.02 ± 0.36	0.00	0.947
	Third test	-0.66 ± 0.3	4.76	0.029
	Mosquitoes			
	Intercept	-1.28 ± 0.35	13.62	0.0002
	Second test	0.32 ± 0.46	0.48	0.488
	Third test	0.49 ± 0.43	1.25	0.263
Deadly attacks	Ants			
	Intercept	-1.34 ± 0.46	8.59	0.003
	Second test	0.85 ± 0.60	2.03	0.154
	Third test	1.14 ± 0.59	3.69	0.055
	Mosquitoes			
	Intercept	-1.34 ± 0.46	8.59	0.003
	Second test	0.12 ± 0.63	0.1	0.753
	Third test	0.38 ± 0.62	0.37	0.541

Effect of temperature and diet on prey consumption and development

The relationship between the number of days spent in the trays and diet varied significantly with respect to temperature (Table 4.2; *P* < 0.0001). *Toxorhynchites haemorrhoidalis* larvae spent less time in the trays when raised with mosquito larvae as food than when provided with ants only (-0.66 ± 0.08, z = -8.08, *P* < 0.0001), and they spent less time at higher temperatures (-0.7 ± 0.08, z = -8.46, *P* < 0.0001). For instance, predatory larvae spent on average 32.7 ± 2.3 and 39.1 ± 4.8 days in the trays at 33°C and 25°C in the mosquito larvae treatment, whereas, when provided only with ants, predaceous larvae stayed twice as long at lower temperature, spending on average 31.4 ± 7.5 and 63.1 ± 13.2 days in the trays at 33°C and 25°C temperatures, respectively. The effect of temperature on the time spent in trays was less marked in the mosquito and in the mosquito-ant diet treatments than in the ant-based diet (Table 4.2).

All individuals died at the larval stage when fed only ants. This weakened our statistical analyses, so we ran subsequent GLMs without this factor (the diet variable remained two-fold: mosquitoes and both mosquitoes and ants). Finally, we detected a marginal but significant effect of temperature on mortality rates (Table 4.2; χ^2, $P = 0.047$). At high temperature, 8 individuals out of 14 died (57%), whereas only 4 died at low temperature (29%). In summary, increasing temperatures significantly reduced the time spent in trays and the survival of *T. haemorrhoidalis*, and this effect was exacerbated by an ant-based diet. At low temperatures, all *T. haemorrhoidalis* larvae (except one that died) developed over a short period of time before emerging when raised only with mosquito larvae as food, whereas they lived twice as long in the trays but they all died before pupation when provided only with ants. At the highest temperature, three individuals died at the larval stage and four were able to emerge when raised only with mosquitoes, while all larvae died over the same time span when fed only with ants.

Table 4.2 Results of the generalized linear models (GLMs) testing the relationship between the number of days spent in trays (Days) and if the Toxorhynchites haemorrhoidalis *larvae pupated or died (Final State) as a function of diet and temperature. Both explanatory variables are factors with three levels. Diet (M):* T. haemorrhoidalis *larvae raised with mosquito larvae only; Diet (M-A): larvae raised with both mosquito larvae and ants; Temp (29): larvae raised at 29°C; Temp (33): larvae raised at 33°C. Only the final models are represented, but Akaike Information Criterions (AIC) are provided for the final model and full models. Dev / rDev = Deviance and residual deviance.*

	Estimate ± SE	Z	*P*	d.f.	Dev / rDev	χ^2	AIC
Days							949.2 (1008)
Intercept	4.14 ± 0.05	87.152	<0.0001				
Diet (M)	-0.66 ± 0.08	-8.08	<0.0001	2	113 / 683	<0.0001	
Diet (M-A)	-0.11 ± 0.07	-1.55	0.12				
Temp (29)	-0.12 ± 0.07	-1.77	0.08	2	34 / 650	<0.0001	
Temp (33)	-0.7 ± 0.08	-8.46	<0.0001				
Diet (M) : Temp (29)	0.05 ± 0.12	0.47	0.641	4	67 / 583	<0.0001	
Diet (M-A) : Temp (29)	0.18 ± 0.1	1.84	0.07				
Diet (M) : Temp (33)	0.88 ± 0.12	7.2	<0.0001				
Diet (M-A) : Temp (33)	0.53 ± 0.11	4.82	<0.0001				
Final State							53.32 (56.72)
Intercept	0.92 ± 0.59	1.55	0.12				
Temp (29)	0.88 ± 0.97	0.91	0.36	2	6 / 47	0.047	
Temp (33)	-1.2 ± 0.8	-1.5	0.13				

Temperature had a significant influence on the daily average consumption of mosquito larvae (Kruskal-Wallis test, $\chi^2 = 8.16$, $P = 0.017$), but not on that of ants (Kruskal-Wallis test, $\chi^2 = 3.04$, $P = 0.22$). A single fourth instar predatory larva could eat up to 339 and 167 third/fourth culicid instars at 33°C and 25°C, respectively (in 67 and 34 d, respectively). By contrast, a single predatory larva could eat up to 41 and 119 ants at 33°C and 25°C, respectively (Figure 4.3).

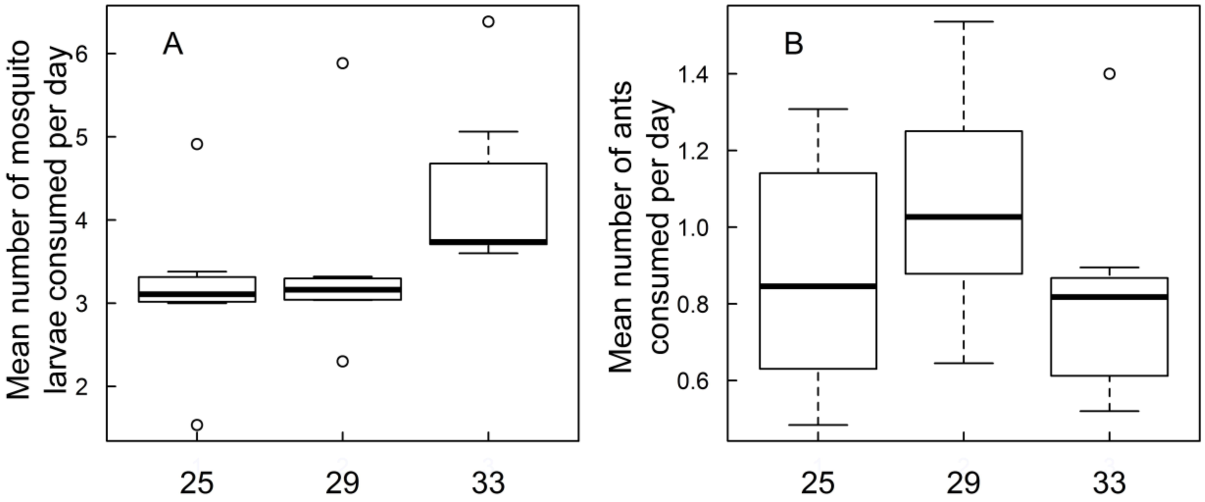

Figure 4.3 Mean number of mosquito larvae (A) and ants (B) consumed per day at 25°C, 29°C, and 33°C. Temperature had a significant effect on the mean daily consumption of mosquito larvae (A) but did not influence ant consumption (B) (Kruskal-Wallis test, $\chi2$ = 8.16, P = 0.017 and $\chi2$ = 3.04, P = 0.22 for A and B, respectively).

Temperature did not significantly affect the pattern of mean daily prey consumption. Indeed, within a given diet treatment (either raised with a single or both prey species), slopes in the various temperature treatments were not significantly different (Table 4.3; Figure 4.4; Kruskal-Wallis tests, $0.07 < \chi^2 < 2.82$, $0.244 < P < 0.965$). By contrast, diet significantly changed consumption rates. For instance, when fed only with mosquito larvae, *T. haemorrhoidalis* larvae greatly increased their prey consumption over time throughout the fourth instar stage (average slope estimates in this treatment = 1.53 ± 0.33 SE), eating up to 10 mosquito larvae per day for several days before pupation or death. However, the average slope of mosquito larva consumption dropped to 0.3 ± 0.07 when the predatory larvae were raised with both mosquito larvae and ants, representing around 3 mosquito larvae per day before pupation or death, and the slopes are significantly different (Table 4.3; Figure 4.4A; Wilcoxon Rank Sum test, W = 409, $P < 0.0001$).

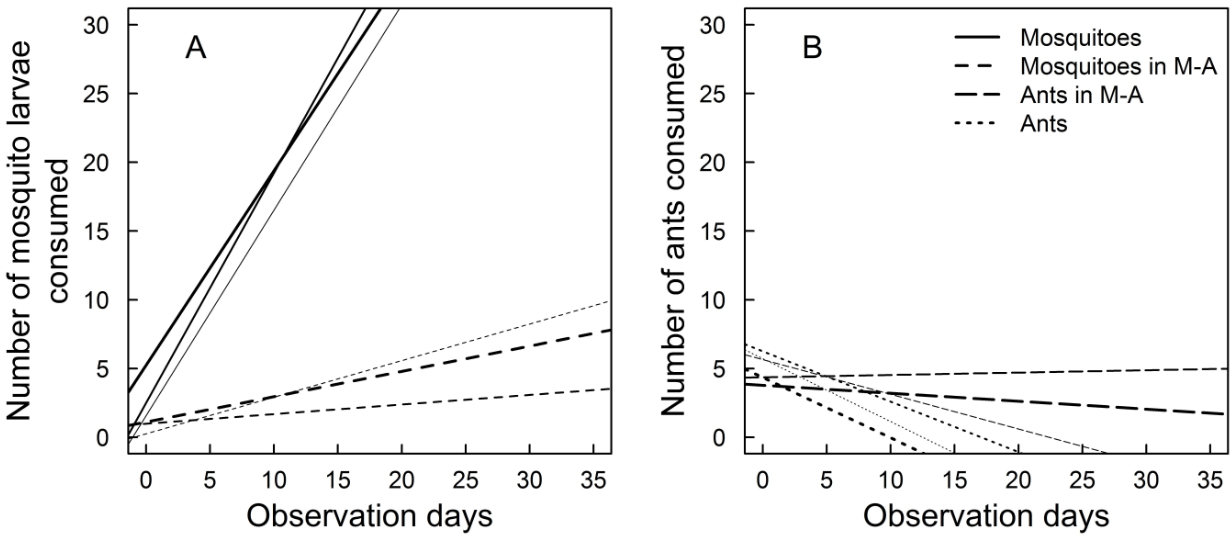

Figure 4.4 Mean slope estimates of the number of mosquito larvae (A) and ants (B) consumed over time according to three temperature and diet treatments. Increasing slope thickness represents an increase in temperature treatment (25°C, 29°C, and 33°C). M-A represents treatments where Toxorhynchites haemorrhoidalis *larvae were provided with both mosquito larvae and ants (see Table 4.3 for SE). Note that observations (x axis) were made every three days. To obtain daily consumption one needs to divide the consumption by three.*

Contrastingly, when provided only with ants, consumption was negatively correlated with time (-0.42 ± 0.1); *i.e.*, less than one ant per day on average before dying. Nonetheless, when provided with both mosquito larvae and ants, the consumption of ants was less negatively correlated (-0.1 ± 0.02); thus, predatory larvae ate more than one ant per day before pupation or death. The slopes for the consumption of ants in the different treatments were significantly different (Table 4.3; Figure 4.4B; Wilcoxon Rank Sum test, W = 98.5, *P* = 0.012). Finally, regardless of the temperature, the dry mass of *T. haemorrhoidalis* pupae fed with both mosquito larvae and ants (3.17 ± 0.9 mg; *N* = 13) was significantly lower than the dry mass of pupae fed with mosquito larvae only (4.48 ± 1.1 mg; *N* =16; W = 161, *P* = 0.01).

Table 4.3 Average slope estimates and standard errors calculated from models where the number of prey consumed by Toxorhynchites haemorrhoidalis *larvae was regressed against time. The slopes are distributed according to nine treatments: three different temperatures (average temperature in Celsius) x three different diets.* T. haemorrhoidalis *larvae were provided with either mosquito larvae or ants alone, or with both mosquito larvae and ants. When* T. haemorrhoidalis *larvae were provided with both mosquito larvae and ants, two slopes were estimated for each prey consumed. The results of Kruskal-Wallis tests (K-W) and Wilcoxon Rank Sum tests (W) are presented.*

	Estimates ± SE	Temperature effect			Diet effect	
		K-W	d.f.	*P*	W	*P*
Mosquito larvae consumed		1.69	2	0.429	409	<0.0001
Temperature (25)	1.49 ± 0.57					
Temperature (29)	1.67 ± 0.63					
Temperature (33)	1.41 ± 0.53					
Mosquito larvae consumed in M-A treatments*		0.831	2	0.67		
Temperature (25)	0.3 ± 0.11					
Temperature (29)	0.19 ± 0.07					
Temperature (33)	0.43 ± 0.18					
Ants consumed in M-A treatments*		2.82	2	0.244	98.5	0.012
Temperature (25)	-0.25 ± 0.1					
Temperature (29)	0.02 ± 0.006					
Temperature (33)	-0.06 ± 0.02					
Ants consumed		0.07	2	0.965		
Temperature (25)	-0.44 ± 0.19					
Temperature (29)	-0.37 ± 0.14					
Temperature (33)	-0.46 ± 0.18					

** M-A represents treatments where predatory larvae were provided with both mosquito larvae and ants.*

DISCUSSION

Gut contents indicate that *T. haemorrhoidalis* larvae living in tank bromeliads in the wild prey upon both small ant species (*i.e.*, *Crematogaster* spp.) and aquatic mosquito larvae. **Paine (1934)** was the first to observe that *T. inornatus* is attracted by any disturbance generated on the surface of the water by aerial insects. Subsequently, **Breland (1949)** suggested that terrestrial insects may be an important food source for *Toxorhynchites* larvae when other prey are unavailable. Our choice tests demonstrated that *T. haemorrhoidalis* larvae preferentially selected terrestrial prey and displayed an active predatory behavior towards ants that included several discrete steps spanning from prey localization to prey manipulation and consumption. This behavior indicates that these larvae are able to process spatial information so as to optimize the acquisition of terrestrial resources **(Linley 1995)**.

Neither active (with ants) nor ambush-like predation (with mosquito larvae) behaviors were affected by temperature manipulation in subsequent experiments.

As insects are ectotherms, their metabolic activity generally increases with temperature and they are capable of adjusting their consumption habits accordingly **(Ward and Stanford 1982)**. Here, *T. haemorrhoidalis* showed a significant increase in the daily consumption of mosquito larvae in relation to the temperature gradient generated (25°, 29° and 33°C). Regardless of the time spent in the trays, these predators ate on average 1.6-times more mosquito larvae at 33°C than at 25°C. These observations are in line with previous studies about consumption rates by *Toxorhynchites* spp. **(Trpis 1972, Steffan & Evenhuis 1981, Lounibos *et al.* 1998)** and other culicid species **(Lounibos *et al.* 2002, Reiskind & Zarrabi 2012)**. By contrast, *T. haemorrhoidalis* larvae ate on average 2.7-times more ants at 25°C than at 33°C. Indeed, these predatory larvae spent more time in trays at 25°C than at 33°C, even though their mean daily consumption of ants was not significantly affected by temperature. These data represent the first reported consumption rates of terrestrial prey by aquatic invertebrate predators in relation to water temperature. Temperature significantly influenced the survival of the late instar larvae through its interaction with diet. Indeed, when fourth instar *T. haemorrhoidalis* larvae were fed only with ants, the individuals died after 31 days at 33°C on average, compared to 63 days at lower temperatures. The larval life span of this genus varies from 10 to 91 days depending on the species, water temperature, and prey density **(Steffan & Evenhuis 1981)**. Although mortality among predatory larvae was high at 33°C, suggesting that this temperature is at the edge of the thermal tolerance range for *T. haemorrhoidalis*, the adults oviposit in both forested and sun-exposed areas in French Guiana (personal observations, see also **Jabiol *et al.* 2009**); thus, the larvae are naturally exposed to extreme temperatures.

Our results also showed that the adverse effect of temperature on the metabolic demands of *T. haemorrhoidalis* was exacerbated by consuming ants. Pupation was never achieved at any temperature on an ant-only diet. It is possible that the ants provided few nutritional rewards compared to the energetic cost of manipulating and digesting them, and/or that they did not provide chemical compounds required to trigger pupation. Assuming that *T. haemorrhoidalis* is well-adapted to preying upon terrestrial insects and that this behavior has not been counter-selected, there must be a threshold of toxicity (*e.g.*, the digestive enzymes and alkaloid compounds of ants' venom) beyond which predators cannot survive. The effect of food toxicity has been well studied in herbivorous species but less so in predators **(Gutierrez-Ibanez *et al.* 2007, Behmer 2009, Jensen *et al.* 2011)**.

Generalist predators are believed to feed on a wide variety of resources to obtain a nutritional balance **(Behmer 2009)**. In this study, regardless of temperature, the dry mass of *T. haemorrhoidalis* pupae fed with both mosquito larvae and ants was significantly lower than the dry mass of pupae fed with mosquitoes only. For many holometabolous insects, reproduction is closely linked to the amount of resources accumulated during the larval stages **(Boggs & Freeman 2005)**. However, the extent to which the morphological and physiological characteristics (*e.g.,* the dry mass of pupae and adults, or wing length; see **Reiskind & Zarrabi 2012**) of pupae are related to adult fitness in *Toxorhynchites* spp. deserves further attention. Learning to distinguish suitable from unsuitable prey coupled with effective foraging techniques can greatly improve fitness **(Cunningham *et al.* 1998, Ishii & Shimada 2010)**. Learning has been reported in several insect taxa, and can even continue after metamorphosis in holometabolous insects **(Dukas 2008, Kawecki 2010)**. Here, we report that ants suffered a higher total number of attacks in the first choice test compared to mosquito larvae, and that this number decreased significantly in the third test. These results suggest that *T. haemorrhoidalis* individuals were more effective at capturing ants on the third day than on the first one, and we cautiously posit that learning may improve foraging efficiency in predatory larvae. In the presence of both mosquito larvae and ants, fourth instar *T. haemorrhoidalis* decreased their consumption of mosquitoes and shifted to ants, whatever the temperature (see Figure 4.4). We thus suggest that throughout its fourth instar stage (long-term basis) and regardless of thermal conditions, *T. haemorrhoidalis* cannot distinguish energetically suitable (mosquito larvae) from unsuitable (ants) prey. We conclude that the stimulus produced by ants on the surface of the water influenced the predator more than the adverse outcome of an ant-based diet. This study provides further evidence that prey activity and/or detectability is one of the main drivers of diet in aquatic invertebrate predators rather than a predator's active choice **(Peckarsky & Penton 1989, Sih 1993)**. Other unexpected consumption habits have been reported by **Eggert and Wallace (2007)**, who showed that some aquatic detritivores preferentially fed upon leaf detritus although the surface biofilm of microbes was more nutritionally suitable. The prevalence of such unexpected behaviors in nature therefore requires greater attention given their importance in helping to predict the effects of disturbances on communities *via* species' responses.

The sophistication of *T. haemorrhoidalis* foraging strategies also indicates that it is well-adapted to prey on terrestrial insects. It may be that under natural conditions (*i.e.,* in the water-filled rosettes of the bromeliads) *T. haemorrhoidalis* preferentially consumes terrestrial prey more nutritious than ants, so that the observed hunting strategy could increase growth. Field experiments manipulating terrestrial invertebrate inputs could test the preference for ants *vs.* other terrestrial species in nature. A related question concerns the frequency at which terrestrial resources enter the aquatic food web. Nevertheless, this study suggests that predatory larvae in bromeliad reservoirs are frequently exposed to ants and preferentially feed on them, despite the higher abundance and constant availability of aquatic prey. The trophic level at which allochtonous resources enter the system is also of great importance as it may enhance either the top-down or bottom-up effects that pervade the entire food web **(Jefferies 2000)**. In tank bromeliads that host *T. haemorrhoidalis* larvae which preferentially feed on terrestrial insects, aquatic invertebrates (notably mosquito larvae) may indirectly benefit from predation release. In conclusion, higher temperatures negatively affect the survival of *T. haemorrhoidalis* through interaction with diet, but do not change *T. haemorrhoidalis* preference for terrestrial prey despite their adverse influence on survival. The potentially synergistic effects of biotic and abiotic stressors (*e.g.,* sub-optimal diet and thermal conditions) on species-specific behavioral traits may hamper our ability to predict community-wide responses to environmental changes.

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Chapitre 5: Functional trait responses of aquatic macroinvertebrates to simulated drought in a neotropical bromeliad ecosystem

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Abstract. The duration of the dry seasons in south-eastern Amazonia is expected to increase. Little is known of how freshwater assemblages respond to drought in the humid rainforests, and of the extent to which they resist the absence of rainfall before the collapse of the system. We manipulated rainshelters over tank-forming bromeliads (*i.e.*, the interlocking leaf axils of these plants form wells that collect rainwater) to simulate an exceptionally long dry period (49 days, compared with a 10-year mean ±SD annual maximum number of 17±5.3 days without rainfall at the study site) and then a rewetting period in a group of treatment plants. We followed the dynamics of the representation of abundance-weighted traits in invertebrate assemblages in treatment and control groups of tank bromeliads by sampling weekly over 3 months. The functional structure of assemblages was drought-resistant until the water volume in the bromeliad pools dropped by 90%, when there was a sudden shift in the functional trait structure due to the loss of most populations except the drought-resistant culicids. Traits related to life history, body size and preferred food showed significant responses to drought. There was a convergence in the functional traits of species surviving in dry plants, strengthening the idea that environmental filtering, rather than stochasticity, determines the functional trajectory of aquatic assemblages during drought. At the end of the dry period, samples of the detritus potentially containing drought-resistant eggs/cysts (and eventually live larvae) were taken from the dry plants and rewetted in the laboratory, allowing us to distinguish resistant species from those requiring recolonisation via subsequent oviposition by adults from elsewhere.. Patches of water-filled bromeliads persisting in the area provided the most important pool of colonists, and communities returned to the pre-disturbance state within 1-2 weeks of rewetting. Our results suggest that the functional trait structure of invertebrate assemblages in bromeliads could remain stable under scenarios of precipitation change that would triple the duration of current dry periods on a local scale. Future experiments should evaluate how environmental factors might alter the tipping point between resistance to drought and a collapse in ecosystem processes.

Keywords: Climate change; food webs; precipitations; rainforests; resilience; resistance; tipping point

INTRODUCTION

Anthropogenic climate change is predicted to increase the frequency and intensity of extreme climatic events such as severe droughts **(IPCC 2013)**. Ecosystems will not only be affected through temperature-related changes in physiological rates **(Sheldon *et al.* 2011)**, but also through disruption of rainfall patterns **(Dejean *et al.* 2011, Naiman & Dudgeon 2011)**. In South America, the northern and eastern coasts and central Amazonia are predicted to become drier (seasonal estimates range from 10-50%), whereas the western equatorial and south-eastern coasts are predicted to become wetter **(Karmalkar *et al.* 2008, IPCC 2013, Magrin *et al.* 2014)**.

The hydrology of freshwater ecosystems is expected to be affected by altered precipitation patterns **(Lake 2011)**, with important consequences on aquatic communities and the ecosystem functions they support **(Sim *et al.* 2013)**. Functional traits, the biological, physiological and ecological attributes of organisms, determine how individuals interact with their environment **(Violle *et al.* 2014)**. Assuming that the biological assemblage of any given ecosystem integrates the spatial-temporal variability of the environment **(Southwood 1988)**, taxa with certain combinations of physiological-ecological adaptations are believed to be selected by the dynamics of the local and regional environment. For instance, macroinvertebrates assigned to functional groups based on life-history strategies and/or on adaptations to acquire food have proven relevant to track changes in ecosystem processes in relation to drought **(Gascón *et al.* 2008)**, while the survival of large-bodied species feeding near the apex of food webs may be particularly affected by drought **(Power *et al.* 2008,**

Bogan & Lytle 2011, Ledger *et al.* 2011). Conversely, traits that confer resistance and/or resilience to drought (*e.g.*, small body size, short generation times, asexual reproduction, eggs, cysts) should be selected through environmental filtering **(Dolédec *et al.* 2006, Sim *et al.* 2013)**. Hence, while models that link environmental conditions to community structure are needed to predict ecosystem responses to drought, the recent literature points towards the idea that knowledge of the changes in the functional traits represented in food webs, rather than changes in species occurrence and/or abundance, will greatly improve our ability to predict the impact of environmental change on ecosystems, and, more importantly, tipping points for any particular ecosystem process, or state **(Statzner *et al.* 2001, McGill *et al.* 2006, Poff *et al.* 2006, Lamanna *et al.* 2014)**.

The absence of rainfall may not translate into immediate ecological responses within freshwater systems, because thresholds in the movement, distribution and/or quality of water that trigger functional shifts depend on the capacity of the system to buffer changes in precipitation. Manipulating rainfall at the whole ecosystem level is impractical in rivers, lakes or ponds, however, so that the methodological advantages of pre-post test design and treatment *vs* control groups conferred by experimental studies are not achievable in large macrocosms. Hence, most of our current knowledge of environmental filtering of functional traits by drought has come from studies of intermittent rivers **(Reznickova *et al.* 2007, Sangiorgio *et al.* 2007)** and temporary wetlands **(Bond *et al.* 2008, Sim *et al.* 2013)**, where authors took the opportunity of seasonal dry:wet cycles to document shifts in trait composition during drying and rewetting phases. In addition, assembling data on the functional traits represented in food webs is a challenging issue; first, because many food webs are too complex or spatially diffuse to allow adequate sampling, and second, because most ecosystem types lack natural replication (even well-delineated ponds and lakes are too diverse to form true replicates). Natural aquatic microcosms such as phytotelmata (water held in plants) form alternative models (reviewed in **Srivastava *et al.* 2004**).

Bromeliads (Bromeliaceae) are flowering plants represented by 3140 species native mainly to the neotropics **(Givnish *et al.* 2011)**. The interlocking leaves of tank-forming bromeliads form rosettes that collect rainwater (from a few millilitres to a few litres). This water source, in addition to leaf litter inputs from the bromeliad itself, provide a habitat for aquatic organisms ranging from prokaryotes to invertebrates which together constitute an aquatic community (see **Brouard *et al.* 2012**). The food webs within tank-forming bromeliads contain several trophic levels, are easy to sample completely, are widely distributed in the neotropics, and are replicated many-fold in nature **(Richardson 1999)**. Owing to these features, these natural microcosms are relevant model systems for investigating the functional response of aquatic communities to disrupted precipitation using manipulative experiments.

Resistance and/or resilience to severe drought is inherent to, for instance, Mediterranean or arid-land communities **(Céréghino *et al.* 2012, Boersma *et al.* 2014)**. However, little is known of how biological communities respond to drought in rainforests, and of the extent to which neotropical communities resist the prolonged absence of rainfall before a tipping point is reached. Our experimental study was conducted in French Guiana (eastern Amazonia). We studied how complete drying and then rewetting affected tank-bromeliad communities in terms of temporal changes in the trait modalities (where a 'modality' is one of a number of categories that a trait can take) represented. We then identified thresholds in community resistance and resilience in relation to drought-induced changes in hydrology. We followed changes in the abundance-weighted traits represented in treatment and control groups of plants over 3 months. Assuming that functional traits reflect environmental conditions that may be shared by many species **(Céréghino *et al.* 2012)**, we expected that (i) either community resistance or vulnerability to drought would result from synchronous response of co-occurring species (*i.e.*, most species resist, decline in numbers or collapse simultaneously), and (ii) environmental filtering would generate a convergence in the functional traits of surviving species under the harshest conditions.

MATERIAL AND METHOD

Study site and bromeliad species

Our experiment was conducted from March 2014 to July 2014, in a lowland rainforest near the Petit-Saut Dam in French Guiana (5°03'43''N, 53°02'46''W; altitude < 80 m). The climate is tropical moist with 3,000 mm of annual precipitation, with little variation in seasonal temperature (monthly averages from 20.5°C to 33.5°C), and relative humidity (70% to 100%). There is a major reduction in rainfall between September and November and another shorter and more irregular dry period in March. A preliminary analysis of daily rainfall records in our study area over the past ten years (see **Dejean *et al.* 2011**) showed that the annual mean ± SD maximum number of consecutive days without rainfall in a dry season is 17±5.3. The only tank-bromeliad species at our study site was *Vriesea splendens*. The vegetative traits, aquatic milieu and invertebrate assemblages in this common bromeliad in French Guiana were described in **Jabiol *et al.* (2009)**, **Brouard *et al.* (2012)**, and **Leroy et *al.* (2013)**.

Experimental design and invertebrate sampling

We selected 12 mature bromeliads (excluding flowering stages) that were similar in terms of their vegetative traits (size, leaf display, number of leaves forming wells, *etc*.). Six of these plants were allowed to collect rain naturally (control), and six were subjected to a ‘drought’ treatment. The water and air temperature were recorded at each visit using digital probes, to verify that there was no significant difference between air and water temperature, *i.e.*, that water temperature was not confounded with water volume. The pH probes could not be used with the smallest water volumes (less than 0.5 mL at the end of the dry phase); therefore, to ensure consistency in methods, the water pH was measured using pH indicator papers (accuracy: 0.3 units; range: 3.9 - 6.9). The mean weekly precipitation at the study site was calculated from daily rainfall records obtained with a rain gauge. The experiment lasted 15 weeks and was divided into two phases. The first phase (seven weeks) consisted in simulating an exceptionally long dry period by installing a rainshelter (transparent plastic tarps) above six treatment plants. This phase ended when the last treatment plant completely dried out (when we could not detect any water in the leaf wells). We then removed the rainshelters, and refilled all treatment plants manually to their maximum water volume with rainwater. This initiated the rewetting phase (eight weeks) where plants were allowed to collect rainfall naturally like the control plants.

The invertebrate species composition and density in each of the 12 plants was monitored weekly. Invertebrate were identified to species or morphospecies and counted directly in the field using magnifying glasses (x6) and a headlamp (all organisms > 0.5 mm), and immediately returned to their original leaf/plant with the corresponding water volume. To sample the water and aquatic invertebrates in the wells (leaf axils) of each plant (excluding the outer, senescent leaves), we used 10-mL to 1-mL micropipettes with the end trimmed to widen the orifice. The actual volume (V, mL) held by each leaf forming a well was measured using a graduated cylinder. This non-destructive sampling technique has already been used successfully by us **(Céréghino *et al.* 2011, Dézerald *et al.* 2013)** and others **(Jocqué *et al.* 2010)**.

Resistant stages vs recolonization in assemblage recovery after drought

At the end of the dry period, a fraction of the fine detritus potentially containing drought-resistant eggs/cysts (and eventually live larvae) was sampled from all dry (treatment) plants and rewetted in test tubes in the laboratory, to allow us to identify the species representing the resistant forms and those requiring subsequent oviposition by adults from elsewhere. A small volume of distilled water (2 mL) was added to the mature leaf axils (*i.e.*, excluding the central reservoir in the process of formation, and the outermost senescent leaves) in each of the six dry plants in order to rewet the fine detritus. This water (ca. 12 mL per plant) was then sucked in and out three times with a micropipette to homogenize the fine detritus, placed in 50 mL test tubes, and brought to the laboratory where the samples were kept at ambient temperature (~25°C). Any live larvae were immediately sorted, identified and counted. The samples were then checked each day for newly hatched larvae (denoting the presence of resistant eggs), which were also identified and counted. Species found in these tubes evidently had the ability to resist drought, whereas other species presumably recolonized the rewetted bromeliads via immigration from the surrounding area.

Macroinvertebrate functional traits and data analyses

The weekly monitoring of invertebrate species composition and abundance allowed us to build a [samples x invertebrate morphospecies] abundance matrix (samples are in rows and morphospecies in columns), where each "sample" is a bromeliad at a given date. The functional traits for each taxon were obtained from our own observations of live and preserved specimens, as well as previous publications **(Céréghino *et al.* 2011, Dézerald *et al.* 2013)**. We focussed on morphological and trophic attributes (*e.g.,* body size, food, feeding habits) as well as life history (*e.g.,* resistant forms, adult stage aquatic or terrestrial, cohort production intervals), these traits being often seen as important drivers of species' responses to droughts **(Fenoglio *et al.* 2007)**. Categories used for the different traits are listed in Table 5.1. Information on the biological traits was then structured using a fuzzy-coding technique **(Chevenet *et al.* 1994)**: scores ranged from '0', indicating 'no affinity' to '3', indicating 'high affinity' for a given trait category. This procedure allowed us to build the [invertebrate species x traits] matrix (invertebrate species are in rows and traits in columns; see also **Dedieu *et al.* 2015**). We then combined both matrices by matrix multiplication to upscale trait information to the community level in the form of a [samples x traits] matrix, where each sample represents a bromeliad at a given date (in rows), and the abundance-weighted traits are in columns **(Pillar *et al.* 2009)**.

If drought impacted the functional trait composition of macroinvertebrate assemblages to some extent, then treatment samples should deviate from control samples in ordination space in terms of the weighted average of their species traits. To test this assumption, and to further identify functional traits that were significantly affected, a Fuzzy Correspondence Analysis (FCA) was conducted on the log-transformed [samples x traits] matrix **(Chevenet *et al.* 1994)**. The aim of the FCA is ordinate the samples according to their abundance-weighted trait modalities, and to schematise variations in the combinations of functional traits of macroinvertebrate communities in the ordination space. The significance of each trait modality to the functional response of the community (axes 1 and 2 of the FCA accounting for 89% of the overall variance, see Results) was then assessed using Pearson correlation coefficients. Mann-Whitney tests were used to test significant differences in sample distribution in the FCA according to control and treatment groups by using coordinates of samples on the most significant axis.

To summarize temporal trends in abundance-weighted trait modalities, and to identify thresholds in community resistance and resilience in relation to drought-induced changes in water level, the mean proportions of abundance-weighted trait modalities were plotted against time for each trait for control and treatment bromeliads. Abiotic difference among treatment and control plants were compared between the beginning (week 1), the dry period (week 5), and the end of the experiment (week 15) using Mann-Whitney and Wilcoxon tests. All uni- and multivariate analyses were conducted using the R software V. 3.2.1 **(R Core Team 2015)**.

RESULTS

Temporal changes in physicochemical variables

The mean daily rainfall (±SD) was 8.68 ± 2.1 mm during the study period. The water volume held by control plants remained almost constant throughout the 15 weeks (90.7 ± 2.9 mL) (Figure 5.1). Treatment plants held 87.9 ± 7.4 mL of water at the beginning of the experiment, and 0.76 ± 0.3 mL after 4.66 ± 0.44 weeks (Figure 5.1a). Owing to the small size and high terrestrial:aquatic surface ratio of bromeliads, water temperature closely followed air temperature and was not affected by our treatment. The difference between water and air temperatures was less than 0.8°C in treatment and control plants, regardless of the experimental phase (Mann-Whitney and Wilcoxon tests, all $W > 18$, all P-values > 0.42). The mean rainwater pH (±SD) was 5.3 ± 0.23 throughout the experiment. However, pH decreased significantly during the drought period in all treatment plants compared to the control ones (mean pH = 4.6 ± 0.07 and 5.0 ± 0.02, respectively; $W = 36$, P-value = 0.004), but were not significantly different at the beginning and at the end of the experiment (all $W > 15$, all P-values > 0.68; Figure 5.1b). Because pH was measured with papers accurate to only 0.3 units and had a relatively small range (3 units), we remain cautious on the significance of this last results. Nevertheless, we note that standard deviations of our estimates did not overlap during the drought phase (Figure 5.1b).

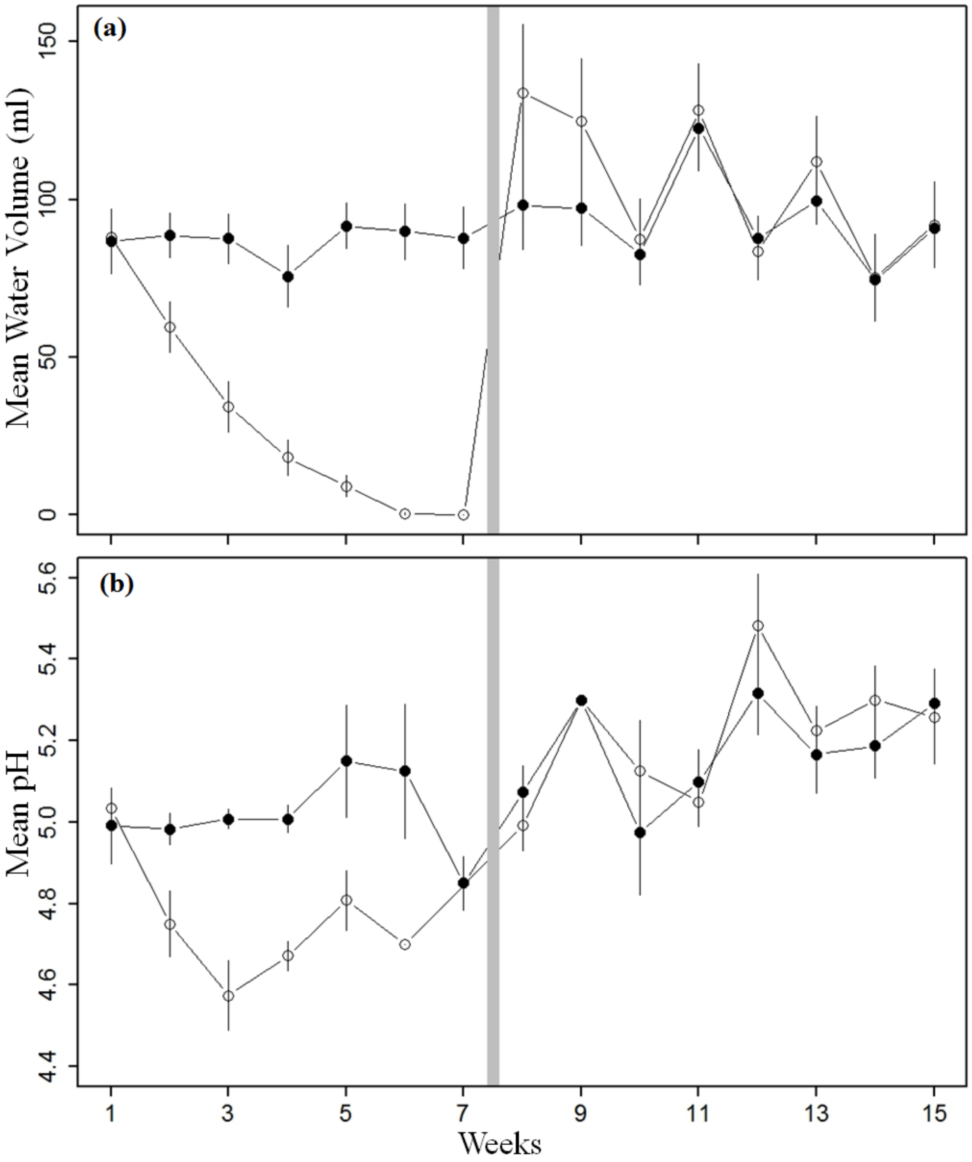

Figure 5.1 Weekly changes in mean (±SD) a) water volume (mL) and b) pH in control and treatment plants (solid and open circles, respectively). The grey bar indicates beginning of the rewetting period (see text).

Fuzzy-coding analysis of species trait combinations

The first and second axes of the FCA explained 76.0% and 13.2% of the total variance in trait composition of the aquatic community, respectively. The first axis (FCA1) displayed a shift in mean community traits from control (right) to treatment plants (left) (Figure 5.2), and there was a significant difference between plant groups (control *vs* treatment) along this axis (Mann-Whitney and Wilcoxon test, W = 1102, *P*-value < 0.0001). The driest samples within the treatment group were located on the left side of the scatterplot. Significant correlations were found between the scores of the first two axes and most trait categories (Figure 5.2).

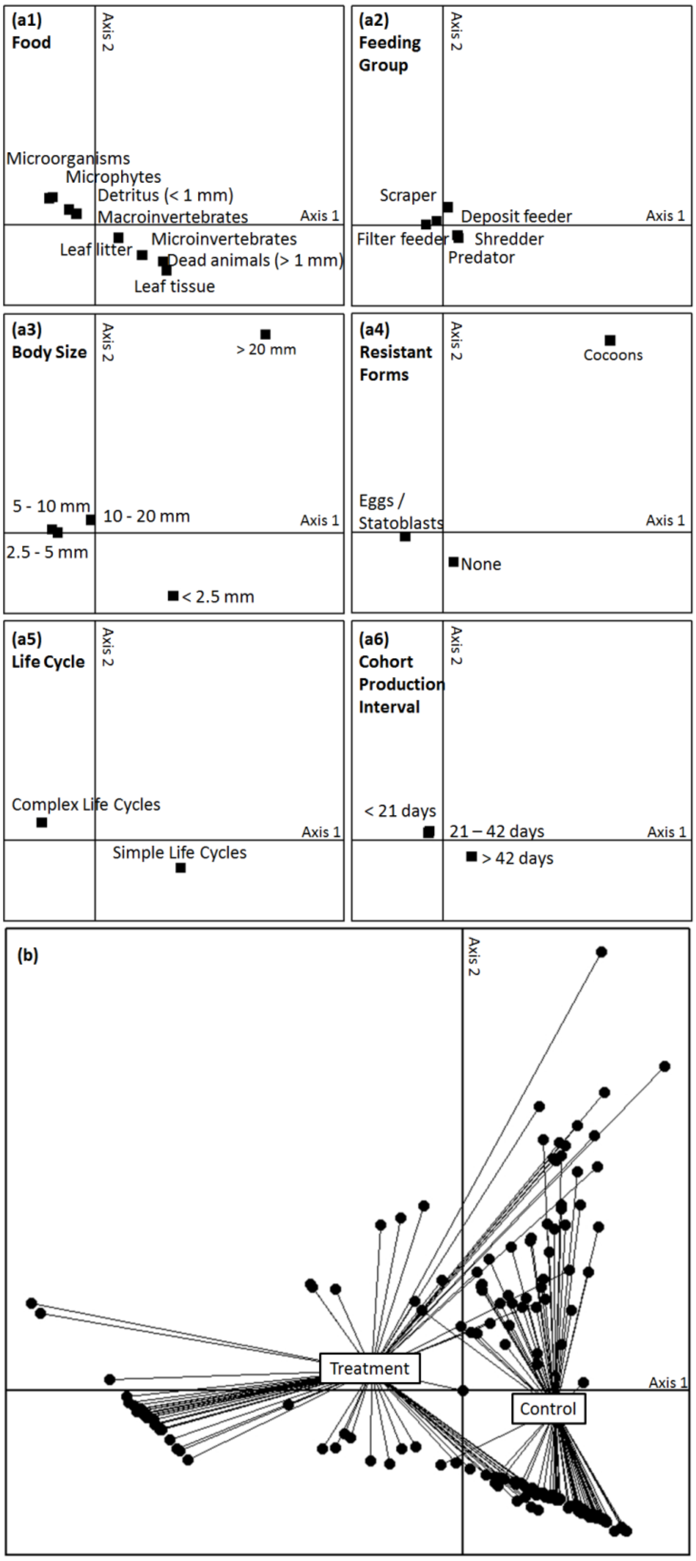

Figure 5.2 Fuzzy correspondence analysis (FCA) of functional trait composition in samples originating from control and treatment plants: a1-a6: distribution of species trait modalities on the first two axes, b) ordination of samples on the first two axes of the FCA, and grouping of samples according to treatment and control bromeliads. Each panel a1 to a6 can be compared to (or supersimposed on) the distribution of samples represented in b), to interpret the set of traits modalities associated with the various areas (or macroinvertebrate communities) of the ordination space. Modalities are positioned at the weighted average of their species.

Overall, traits related to life history (cohort production interval, life cycle type, resistant forms) and food preference were the most significant on the first axis, while traits related to body size and resistant forms showed gradients along the second axis (Kendall’s Tau coefficient tests, see Table 5.1).

Table 5.1 Functional traits, trait modalities and functional trends (‘+’= increase or ‘-’= decrease with decreasing effect of drought) resulting in a significant Kendall’s Tau coefficient between the proportion of trait modalities and the first and second axes scores in the Fuzzy Correspondence Analysis.

Biological traits	Trait Modality	Modality ID	First axis		Second axis	
			Tau	*P*-values	Tau	*P*-values
Food	Microorganisms	Food1	-0.76	***	0.37	***
	Detritus (< 1 mm)	Food2	-0.56	***	0.27	***
	Leaf litter	Food3	0.66	***	-0.39	***
	Microphytes	Food4	-0.76	***	0.41	***
	Leaf tissue	Food5	0.76	***	-0.4	***
	Dead animals (> 1 mm)	Food6	0.80	***	-0.39	***
	Microinvertebrates	Food7	0.64	***	-0.39	***
	Macroinvertebrates	Food8	-0.45	***	0.15	**
Feeding Group	Deposit feeder	Feed1	-0.05	ns	0.13	*
	Shredder	Feed2	0.35	***	-0.4	***
	Scraper	Feed3	-0.16	**	0.19	***
	Filter feeder	Feed4	-0.32	***	0.02	ns
	Predator	Feed5	0.34	***	-0.3	***
Body Size	< 2.5 mm	Body1	0.67	***	-0.48	***
	2.5 – 5 mm	Body2	-0.66	***	-0.05	ns
	5 – 10 mm	Body3	-0.69	***	-0.18	ns
	10 – 20 mm	Body4	-0.15	**	0.03	ns
	> 20 mm	Body5	0.13	*	0.77	***
Resistant Forms	Eggs/Statoblasts	Rstt1	-0.57	***	-0.14	**
	Cocoons	Rstt2	0.13	*	0.77	***
	None	Rstt3	0.37	***	-0.78	***
Life Cycle	Adult stage terrestrial	Life1	-0.94	***	0.26	***
	Adult stage aquatic	Life2	0.94	***	-0.26	***
Cohort Production Interval	< 21 days	Coht1	-0.71	***	0.31	***
	21 – 42 days	Coht2	-0.64	***	0.35	***
	> 42 days	Coht3	0.71	***	-0.34	***

Kendall’s Tau coefficient tests; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns not significant.

There was a higher proportion of organisms with aquatic immature stages and terrestrial adults and with short generation times in treatment plants, as well as those feeding upon microorganisms, microphytes, and fine detritus < 1mm in size. This is consistent with the presence and numerical dominance of *Wyeomyia* culicids in the treatment samples (see below). The centroid of the treatment samples in the ordination space is shifted to the left area of the FCA axis 1, compared to the centroid of the control samples. By superimposing Figure 5.2a.5 and Figure 5.2b, it becomes apparent that treatment samples are characterized by organisms with aquatic larvae-pupae and terrestrial adults, *e.g., Wyeomyia* culicids. Conversely, control samples had higher proportions of organisms with both aquatic immature and adult stages among which the very abundant *Aulophorus superterrenus* (Haplotaxida, Naididae) and *Elpidium bromeliarum* (Podocopida, Lymnocytheridae) were dominant (Figure 5.2a.5 & Figure 5.2b). Assemblages in these plants were also characterized by higher proportions of species with longer generation times, which fed either upon leaf litter or other invertebrates (Fig 5.2a.6 & Fig 5.2a.1, respectively; Fig 5.2b).

Temporal changes in abundance-weighted trait modalities

In the control group, the proportions of abundance-weighted modalities in each functional trait remained almost constant over the 15-weeks experimental period (Figure 5.3a, c, e, & 5.4a, c, e). This finding also suggests that our weekly visits and resampling of invertebrates did not generate a bias in the observed patterns. In the treatment group, the distributions of trait modalities were not affected during the first five weeks of drought, when they remained similar to those observed in the control group. This pattern means that communities resisted drought, despite a large (89.8%) decrease in water volume available. In the sixth week, when the available water volume dropped to less than 1mL (*i.e.,* a 99% decrease compared to the initial volume), only two culicid species, *Wyeomyia* (*Dodecamyia*) *aphobema* and *Wyeomyia* (*Hystatomyia*) *lamellata* were found active in the bromeliads. These species are both filter and deposit feeders, characterized by short generation times (< 21 days) and with complex life cycles. The final instar larvae are < 10 mm in length, and adults lay drought-resistant eggs (see below). Proportions of these trait modalities therefore peaked at 6 weeks (Figure 5.3 & 5.4), while other trait modalities disappeared. In the seventh week, all treatment plants dried out. After refilling the plants with rainwater, within less than two weeks there was a return to a distribution of trait modalities, similar to that in controls, so that assemblages recovered rapidly. The rest of the rewetting phase (weeks 8-15) was characterized by a steady proportion of abundance-weighted trait modalities, much like in control plants. Our results mainly illustrate changes in the relative proportion of trait categories, but proportions can remain almost constant if co-occurring species/traits increase or decrease in abundance simultaneously.

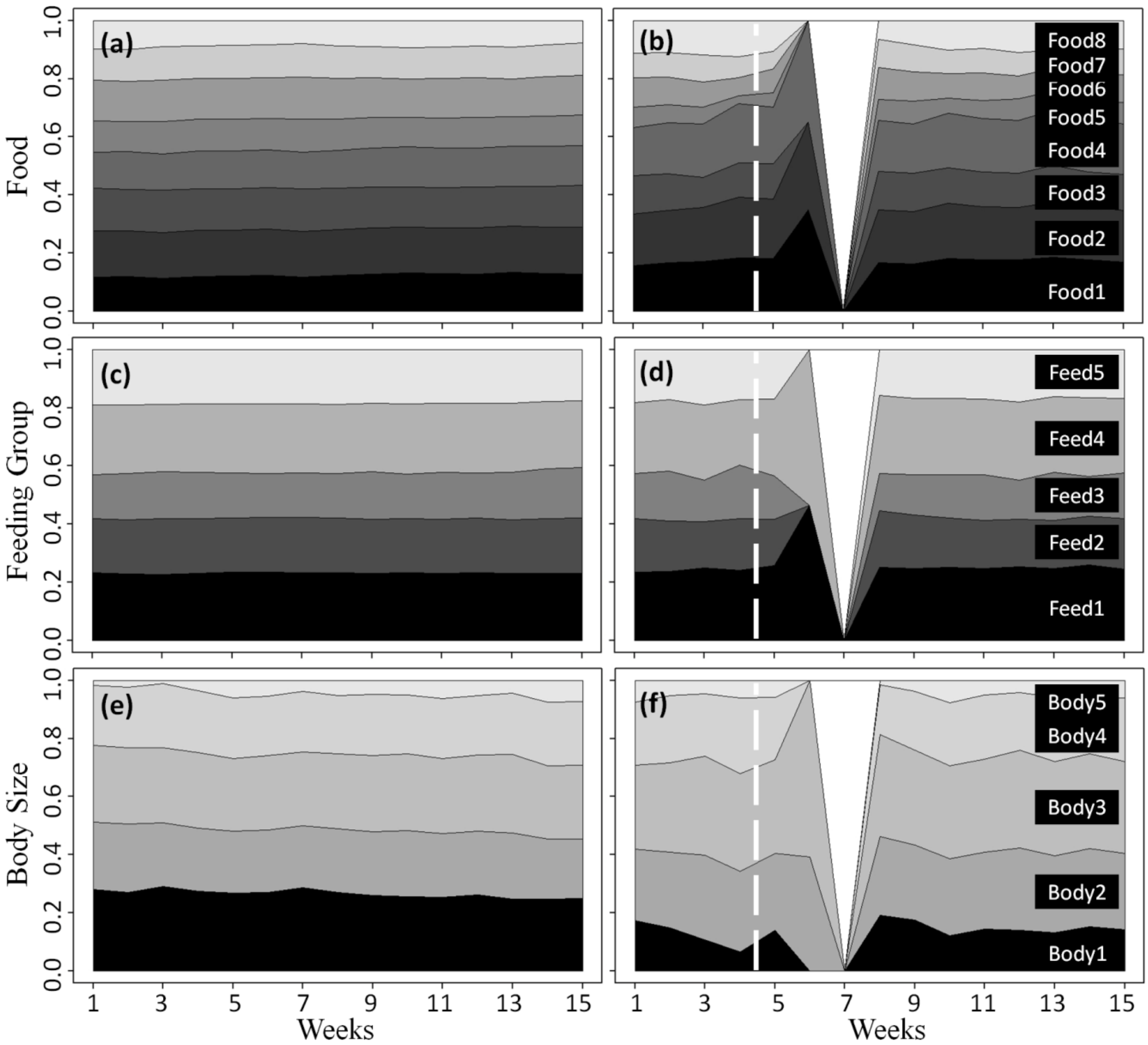

Figure 5.3 Changes in the mean proportions of abundance-weighted traits in control (left panels; a, c, e) and treatment plants (right panels; b, d, f) over time: a, b = food; c, d = functional feeding groups; e, f = body size. Abbreviations in black boxes are the identities of trait modalities as in Table 5.1. The dotted line indicates when the simulated drought had persisted for twice as long as the usual prevailing dry periods in the area.

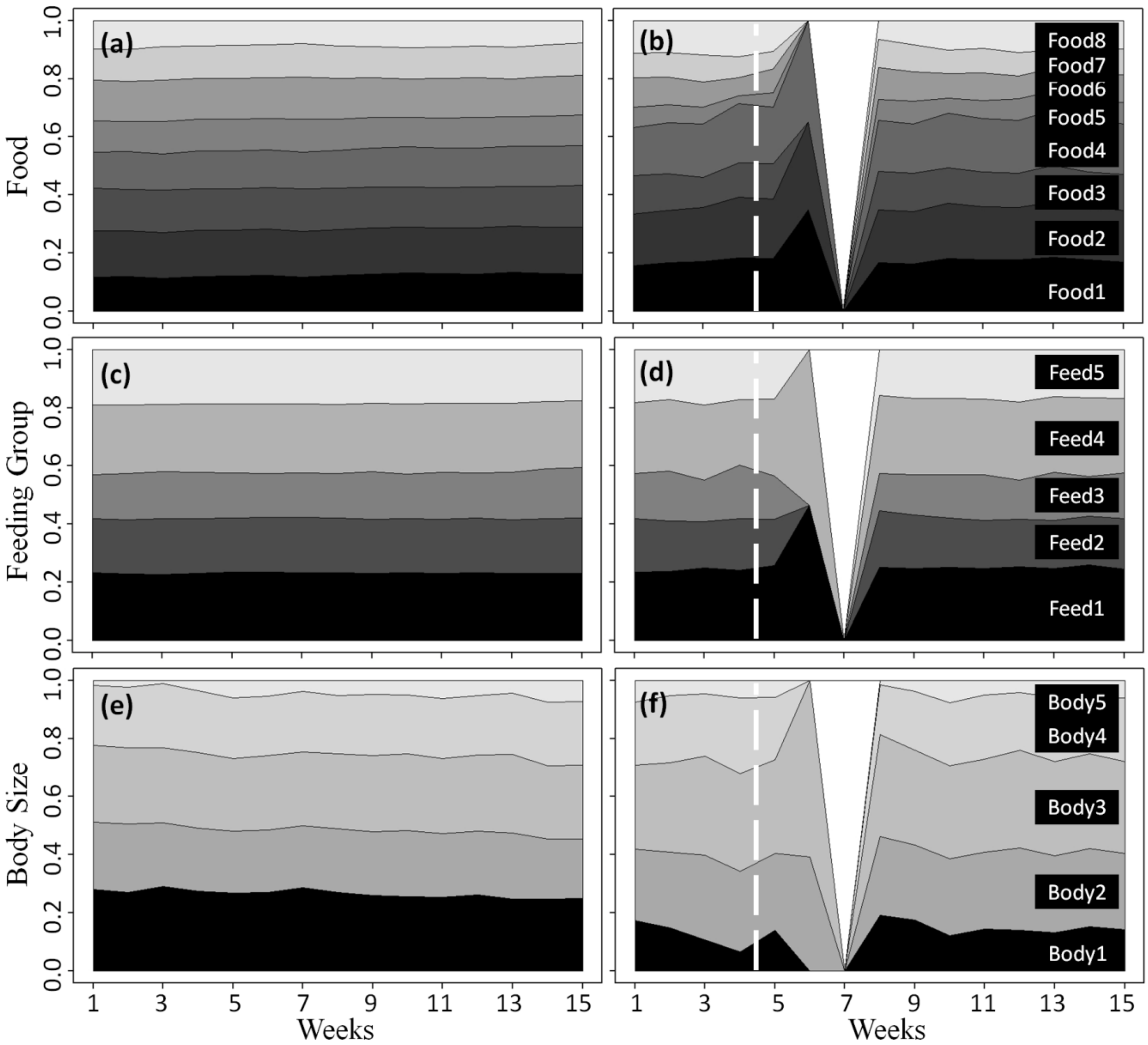

Figure 5.4 Changes in the mean proportions of abundance-weighted traits in control (left panels; a, c, e) and treatment plants (right panels; b, d, f): a, b = resistant forms; c, d = life cycle; e, f = cohort production interval (CPI, days). Abbreviations in black boxes are the identities of trait modalities as in Table 5.1. The dotted line indicates when the simulated drought had persisted for twice as long as the usual prevailing dry periods in the area.

Resistant stages vs recolonization in assemblage recovery after drought

The local taxon pool was composed of 22 morphospecies (Table 5.2). Seven of these taxa were found in tubes that contained rewetted detritus taken from the completely dry plants at week 7 (Figure 5.5). Among these seven taxa, only *Wyeomyia* (*Dodecamyia*) *aphobema* and *Wyeomyia* (*Hystatomyia*) *lamellata* hatched as first instar larvae in our tubes a few days after collecting the detritus, revealing that these species lay drought-resistant eggs in bromeliads.

Table 5.2 The aquatic macroinvertebrates forming the species pool at our study site.

Order	Family	Species
Diptera	Culicidae	*Wyeomyia aphobema*
		W. lamellata
		W. robusta
		Microculex stonei
		Anopheles nevai
		Toxorhynchites sp.
	Corethrellidae	*Corethrella* sp.
	Ceratopogonidae	*Bezzia* sp.
		Ceratopogonidae sp1
		Ceratopogonidae sp2
		Ceratopogonidae sp3
	Chironomidae	Orthocladiinae sp.
		Tanypodinae sp.
		Tanytarsinae sp.
	Tipulidae	*Trentepohlia* sp.
	Psychodidae	*Telmatoscopus* sp.
		Brachycera spp.
Odonata	Coenagrionidae	Coenagrionidae sp.
Coleoptera	Scirtidae	*Cyphon* sp.
Hemiptera	Veliidae	*Paravelia* sp.
Podocopida	Limnocytheridae	*Elpidium bromeliarum*
Haplotaxida	Naididae	*Aulophorus superterrenus*

The five remaining morphospecies were already present as active larvae in the detritus, revealing their ability to survive drought at this stage. *Elpidium bromeliarum* ostracods and both *Wyeomyia* culicids were the dominant species (Figure 5.5). There was less than one individual per plant on average of *Cyphon* sp., *Corethrella* sp., Ceratopogonidae sp1 and Orthocladiinae sp. Other species present in the local species pool were not found in tubes containing rewetted detritus. Therefore, the latter species probably colonize the bromeliads through adult oviposition and/or phoresy after rewetting.

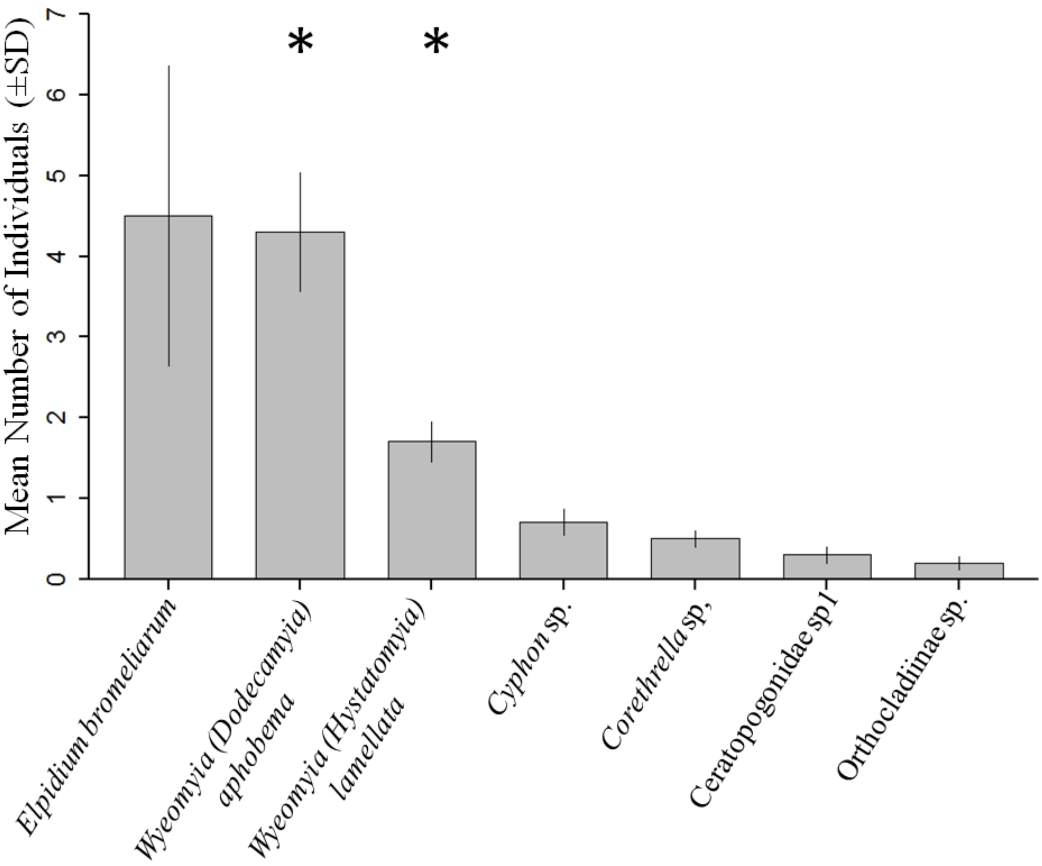

Figure 5.5 Invertebrate species found in rehydrated samples, ranked by decreasing mean (±SD) abundance (from left to right). Asterisks indicate species that hatched from drought-resistant eggs (see text).

DISCUSSION

Intensification in the tropical Atlantic north-south sea surface temperature gradient is expected to enhance the duration of the dry seasons in south-eastern Amazonia, including the Guiana Shield **(IPCC 2013)**. In our study, we created conditions that simulated the impact of a 49-day long drought on neotropical invertebrate communities, *i.e.*, about three-times the maximum number of consecutive days without rainfall under ambient climate. This study is original because we followed the community trait structure over time, thus allowing us to determine possible tipping points in ecosystem processes in relation to hydrological thresholds. Our results showed that the functional structure of communities was drought-resistant until the water volume in the bromeliads dropped by 90%. Beyond this point, there was a sudden shift in the trait structure of communities due to the loss of most populations, except the drought-resistant culicids, and then communities returned quickly to the pre-disturbance state during the rewetting period, suggesting strong resilience.

At our study site, it took up to 7 weeks to dry out a mature *V. splendens* in the understorey. **Zotz & Thomas (1999)** found that *Guzmania monostachya*, an overstorey bromeliad of similar leaf display and water volume, dried out in less than 10 days in Panama, suggesting that the relationship between rainfall and hydrology in bromeliad pools depends both on study locations and bromeliad species. Regardless of the time needed to dry out a plant, the biological diversity of the system was expected either to decrease gradually with increasing drought severity/duration (drought vulnerability hypothesis), or to remain more or less constant until an abrupt shift occurred (drought resistance hypothesis; **Boersma *et al.* 2014**). The stability in the proportion of abundance-weighted trait modalities during the dry phase of our experiment supports the drought resistance hypothesis of bromeliad invertebrate communities in the understorey of a neotropical forest. Interestingly, treatment samples that represented the harshest environmental conditions (end of the dry phase) showed the lowest dispersion in ordination space in terms of the weighted average of their species traits (left area of FCA axis 1 in Figure 5.2b), indicating that: (1) species from the local pool that were unable to withstand severe drought were eliminated, and therefore, (2) environmental filtering led to a convergence in the functional traits of surviving species. We indeed observed that most species declined progressively in numbers during drought until only the most resistant species remained (*Wyeomyia* culicids), suggesting that the taxonomic structure of communities is vulnerable to drought, and strengthening the idea that niche-selection filtering rather than stochasticity determines the functional trajectory of communities during drought **(Chase 2007)**.

Trait modalities related to life history (life cycle type, cohort production interval, resistant forms), morphological attributes (body size) and preferred food did well at discriminating communities from the control and treatment group of plants. To some extent, the significant responses of most traits to drought (Table 5.1) may reflect coincidence among traits within groups of taxa. For instance, long-lived organisms (Coleoptera Scirtidae, Diptera Tipulidae) also processed coarse detritus **(Merritt *et al.* 2008)**. Incidentally, these species tended to decline first, and this may have temporarily decreased decomposition rates in tank bromeliads.

Along with habitat contraction during dry periods, invertebrates faced changes in their chemical environment. The pH declined during drought in treatment plants, but the influence of pH on invertebrate occurrence (notably aquatic insects) could vary among taxonomic groups **(Clark *et al.* 2004)** and could not be ascertained here. We note, however, that the range of pH recorded in our plants remained within the limits of pH values measured with WTW® probes in un-manipulated, water-filled *V. splendens* in French Guiana (4.3 – 5.6, personal observations). An important environmental variable that was not taken into account for technical reasons was dissolved oxygen (O_2). Probes were inefficient at measuring O_2

concentrations in small volumes; however, measurements with WTW® probes in other *Vriesea splendens* in the area revealed that O_2 concentrations varied between 50 and 7%. Assuming a decrease in dissolved O_2 with habitat contraction, we note that the community was dominated by species breathing with a siphon in drying plants (Culicidae), whereas individuals breathing with caudal lamellae and/or tegument were eliminated (*e.g.*, odonates, tipulids). Finally, although this aspect was not investigated in this study, changes in species interactions are likely to moderate the response of functional traits to drought. The concentration of individuals in smaller water volumes might notably increase antagonistic interactions **(Srivastava 2006)**, thus selecting traits related to competition, predation and/or predator avoidance **(Hammill *et al.* 2015)**.

During the rewetting period, communities could respond in two possible ways, *i.e.*, return to a pre-disturbance state, demonstrating resilience, or shift to a new equilibrium **(Bogan & Lytle 2011)**. In our study, the functional structure of aquatic communities returned to the pre-disturbance state in 1-2 weeks after removal of the rainshelters, suggesting a strong resilience to an exceptional drought event, much like other invertebrate communities elsewhere, for instance in streams **(Boulton 2003, Lake 2003, Sim *et al.* 2013)**. The rapid community resilience in our treatment plants can be explained by behavioural and physiological responses to drought, on the one hand, and by environmental conditions that fostered recovery on the other.

In terms of species' responses, the rewetting of dried out detritus in test tubes showed that only a few species are able to survive in residual moisture and withstand dehydration in the active larval or adult stage. This applies notably to the ostracod *Elpidium bromeliarum* (Lymnocytheridae; **Lopez *et al.* 2005**). The production of drought-resistant eggs in *Wyeomyia* species (here *Wyeomyia* (*Dodecamyia*) *aphobema* and *Wyeomyia* (*Hystatomyia*) *lamellata*) is not common, and is new for bromeliad-dwelling *Wyeomyia* (see **Juliano & Lounibos 2005**). The set of species found in our rehydrated samples represented the main sources of 'internal resilience' in the system, while those species not found in our test tubes may have responded to the dry phase by simply leaving bromeliad pools by emerging or crawling, or by dying. Our methods did not allow us to clearly separate mortality from behavioural response to drought **(Williams & Hynes 1974)**. However, we know that some bromeliad-dwelling invertebrates, notably Scirtidae (*Cyphon* sp.), odonates (Coenagrionidae) and Tipulidae (*Trentepohlia* sp.), are able to move from leaf to leaf to find water (personal observations). Owing to their typical dispersal mode, and whatever their response during the dry phase, we conclude that this second set of species contributed to the 'external resilience' of the system, in that they mostly recolonized rewetted bromeliads through adult oviposition (*e.g.*, Culicidae with very short generation times such as *Anopheles neivai*, *Microculex stonei*), and through phoresy (*e.g.*, *Aulophorus superterrenus*, Annelida, see **Lopez *et al.* 2005**). Most organisms gradually recolonized treatment plants over time, until the assemblage and food web structure did not differ from that of the control plants in terms of species composition and abundance. However, not all species recovered at a similar rate. Within the first two weeks of rewetting, filter-feeders, notably *Wyeomyia* species, outnumbered other species. Conversely, Corethrellidae (the numerically dominant predator in control plants) returned to their pre-disturbance density in about five weeks.

Finally, in terms of environmental conditions that fostered resilience, we acknowledge that both control and other un-manipulated bromeliads in the study area certainly provided a substantial pool of colonists. It is likely that the external source of colonists would be depleted and the rate of recovery less rapid if the whole forest (all bromeliads in the area) was subjected to an exceptionally severe drought. This situation compares to that of perennial wetlands that contribute species to seasonal wetlands in regions with a Mediterranean climate **(Sim *et al.* 2013)**, and to immigration from source patches that prevents extinction in sink populations **(Holyoak 2000)**. The effects of real droughts on the potential resilience of invertebrate communities would thus depend upon the spatial extent of droughts (local or extensive) compared to the spatial scale of our experiment, but also on the patchiness of the disturbance (*sensu* **Lopez-Hoffman *et al.* 2013**). For instance, drought-induced tree mortality can be patchy within forests **(Breshears *et al.* 2005)**, resulting in heterogeneous impacts on the understorey environments in terms of evaporation rates, humidity, throughfall upon rewetting, *etc*. Assuming that we would be able to experimentally dry up a larger portion of the forest or a larger number of bromeliad patches, we expect that the functional traits associated with invertebrate species' resistance to drought in bromeliads (this study) would remain unchanged. Typically, most species would resist a 90% decline in water volume available in their individual bromeliads, and culicid would certainly withstand a 99% decrease in water volume whatever the spatial extent of drought. However, because the rates (and predictability) of recolonization strongly depend on the extent of source patches, we would expect resilience time and/or capacity to decrease with an increasing spatial extent and patchiness of disturbance.

In conclusion, although uncertainties remain as regards resilience patterns (see above), the results of our manipulative experiment predict that the trait structure of bromeliad invertebrate communities could remain stable under scenarios of precipitation change that would triple the duration of current dry periods on a local scale. Once we account for variation in bromeliad hydrology during dry periods (*i.e.*, for a fixed decrease in water level), however, it is likely that spatial variations in community structure (*e.g.*, presence or absence of large-bodied predators) with local environmental conditions (*i.e.*, open *vs* closed forest canopies) will mediate the tipping point between resistance to drought and a collapse in ecosystem processes. For instance, **Brouard *et al.* (2012)** compared the detrital food web of understorey bromeliads (forest sites, as in this study) and the detrital-algal-based food web of overstorey bromeliads (sun-exposed) in French Guiana. Not only did these authors suggest that the main trophic pathways are different in these two types of bromeliads, but they also highlighted a higher density of large-bodied predators (odonates, *Toxorhynchites* Diptera) and a lower density of filter-feeders (*Wyeomyia* culicids) in sun-exposed bromeliads (see also **Dézerald *et al.* 2013**). Where bromeliad-dwelling odonates are common, they strongly influence community structure through top-down effects **(Petermann *et al.* 2015)**, but they are more sensitive to desiccation than their common prey (*e.g.*, culicid and chironomid larvae). Hence, one may assume that important functional shifts should occur earlier during the dry phase in an overstorey bromeliad than in an understorey bromeliad. Assuming that communities resist drought for a few weeks before drastic functional shifts occur in the system, further experimental study would therefore be needed to determine the extent to which species turnover and food web structure determine this tipping point.

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Chapitre 6: Context-dependence in the response of Neotropical arthropods and amphibians to simulated precipitation regimes along a biogeographic gradient

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Abstract. The magnitude and frequency of extreme precipitation/drought events in the neotropics is expected to increase in the future. We lack however a multi-regional theory of how these changes will affect species assemblages and ecosystems. When experiments highlighted direct and/or indirect effects in one location, these responses may however not translate to other locations when species show biogeographic turnover in composition and traits. We manipulated the amount and frequency of rainfall intercepted by water-filled bromeliads during 2 months, at three sites ranging from the Caribbean (Puerto Rico) to South-America (French Guiana, Brazil-Macae). Every day, we recorded the occurrence of keystone arthropod (spiders, ants) and amphibian species (frogs) on each bromeliad that corresponded to a rainfall treatment. These animals use tank-forming bromeliads as wet refuges, nesting sites, and/or foraging sites, and represent contrasted sets of functional traits that determine how species interact with their environment. The relationship between the total occurrence (the sum of daily occurrences on a given plant/treatment) of these taxa on bromeliads and the various precipitation treatments was strongly constrained by the study location. Drier sites (Macae) with comparatively smaller species pools were more impacted. Then, at each site, hydrological stability in the bromeliads (rather than precipitation *per se*) and biotic interactions with other taxa were the most influential variables on species occurrences. Daily occurrences of spiders were mediated by frog occurrences and *vice versa*, whereas ants were the least responsive taxa to either precipitation change or biotic interactions with other members of the community. Despite the obvious context-dependence in the direction and magnitude of the biological response, species consistently responded to the hydrological stability of the study system that determines its buffering capacity against changes in rainfall patterns. At the same time, antagonistic interactions could force species to move to less suitable conditions. These results enhance our ability to make community-wide predictions in unstudied portion of the biogeographic gradient.

Keywords: rainfall distributions; hydrological stability; biotic interactions; arthropods; amphibians; tank bromeliads; neotropical rainforest

INTRODUCTION

Ecological impacts of global environmental changes (GEC) occur at all biological (from individuals to ecosystems) and spatial (from local to continental) scales. One of the most consistent GEC forecast is the increase in magnitude and frequency of extreme events **(IPCC 2013)**. For instance, in South America, the northern and eastern coasts and central Amazonia are predicted to become drier (seasonal estimates range from 10-50%), whereas the western equatorial and south-eastern coasts are predicted to become wetter **(Karmalkar *et al.* 2008, Magrin *et al.* 2014)**. Both extreme dry and wet scenarios will have direct effects on species behavior, physiology, phenology, and distribution **(Forrest 2015)**, but also indirect effects mediated by the networks of interacting species **(Henri *et al.* 2012)**. Disentangling these direct and indirect mechanisms is a major challenge **(Winder & Schindler 2004)**. However, when community- to ecosystem level responses to climate change are known for one location, these responses may not translate to other locations when species show biogeographic turnover in composition and traits. In addition, because most hypothesis-driven studies of the ecological outcomes of climate change were conducted on a limited number of species/biotic interactions and considered a small range of precipitation scenarios **(Woodward *et al.* 2010b)**, ecologists tend to accumulate collections of case studies, *i.e.*, context-dependent predictions.

The habitat properties specific to any ecosystem type further intensify context-dependence in the response of organisms to various precipitation scenarios **(Leuzinger & Koerner 2010, Knapp *et al.* 2015)**. These habitat properties in the form of the size, boundary complexity, volume-to-surface ratios and inertia, are likely to buffer variations in precipitation inputs **(Dézerald *et al.* 2015a, Marino *et al.* in prep)** resulting in differential hydrological stability across ecosystems (*e.g.*, the movement, distribution and/or quality of water in aquatic habitats; evaporation, soil infiltration rates and water storage capacity in terrestrial ones). While the effects of precipitation scenarios on biological communities have been explored in both terrestrial and aquatic ecosystems, to date, too few studies have explicitly investigated the combined effects of various precipitation scenarios, habitat properties, hydrological stability, and biotic interactions over broad biogeographic scales (but see **Marino *et al.* in prep**). In other words, little is known about those changes in ecological variables (abiotic and/or biotic) that species are actually tracking or are more sensitive to, either within or across study locations. Investigating such a high level of complexity is challenging. Meaningful insights can be obtained from meta-analyses despite their criticized lack of consistent methodology whereas large-scaled observational studies suffer from low explanatory and predictive power in the absence of experimentation **(Hewitt *et al.* 2007, Gurevitch & Mengersen 2010, Borer *et al.* 2014)**. Additionally, experimentations in large, species-rich and complex ecosystems often raise numerous technical challenges.

To tackle these issues, we manipulated the amount and frequency of rainfall intercepted by water-filled bromeliads (see below) at three study sites ranging from the Caribbean to South-America, measured the resulting changes in hydrological stability of the system, and studied the behavioral response of functionally important and widely distributed arthropods (spiders, ants) and amphibians (frogs) that use tank bromeliads as wet refuges, nesting sites, and/or foraging sites **(Frank & Lounibos 2009, Hénaut *et al.* 2014)**. Importantly, these taxa represent contrasted sets of functional traits that determine how species interact with their environment. Tank bromeliads are flowering plants belonging to the Bromeliaceae family **(Givnish *et al.* 2011)**, and are naturally replicated throughout Central and South America. The foliar architecture of these plants enables each leaf base to form a reservoir or tank that permits accumulation of rainwater and detritus. Thus, these tank bromeliads provide suitable aquatic habitat for a more or less specialized set of species to develop and complete their life cycle. Then, most of these bromeliad-dwelling aquatic invertebrates are exported to the terrestrial environments through adult emergence **(Dézerald *et al.* in prep)**, to the benefit of terrestrial food webs, predators in particular **(Romero & Srivastava 2010)**. Hence, spiders, ants, and frogs mainly rely on these miniature aquatic habitats as foraging and/or nesting sites **(Gonçalves-Souza *et al.* 2011, Talaga *et al.* 2015)**. In turn, their presence is beneficial to both the plant itself and the aquatic communities as they damp nutrient-rich wastes inside the tanks **(Romero 2006, Leroy *et al.* 2015)** or act as efficient phoretic dispersal agents for many aquatic organisms **(Lopez *et al.* 1999, Sabagh & Rocha 2014)**. Although it is well established that these taxa rely on tank bromeliads, the extent to which they can mutually influence each other is unknown (but see **Gillespie & Reimer 1993, Halaj *et al.* 1997, Nelson *et al.* 2004** for antagonistic interactions between ants and spiders).

Our main objectives are i) to assess how relevant ecological variables (*e.g.*, rainfall distribution, habitat properties, hydrological stability, biotic interactions) interact to affect the habitat-selection by bromeliad-dwelling ants, spiders and frog, and ii) to determine whether this response is dependent on biogeographic location or is a general feature of these contrasting sets of species. If biotic interactions are not important in driving species behavior/occurrences on plants, we hypothesized that more stable rainfall distributions and hydrological dynamics would be selected, to some extent, by all taxa. If biotic interactions (*e.g.*, competition, predation) play significant role, species may be forced to displace their environmental preferences to less suitable conditions depending on whether other species are present or not. Finally, assuming that each location induces some amount of variability in the direction (sign) and magnitude of the response, we predicted that still, species may consistently respond to particular ecological factors regardless of study location.

MATERIAL AND METHODS

Study sites and bromeliad species

We selected three sites distributed from the Caribbean to South America. The first site was the Luquillo Experimental Forest (LEF), El Verde, Puerto Rico (18.30°N, 65.79°W, 295-980 m asl). Mean monthly temperatures and rainfalls fluctuate between 18-25°C and 150-600mm, respectively. The experiments were conducted from March to May 2014. The second site was a lowland rainforest near the Petit-Saut Dam in French Guiana (5.03°N, 53.02°W, < 80 m asl). The climate is tropical moist (mean monthly temperatures and rainfalls: 20.5-33.5°C and 40-600 mm, respectively). The manipulations took place from November 2012 to January 2013. The third site was in the northeast of Rio de Janeiro State (hereafter Macae), Parque Nacional da Restinga de Jurubatiba (PNRJ), southeastern Brazil (22.38°S, 41.75°W, < 10 m asl). The climate is tropical moist (mean monthly temperature and rainfalls: 21.7-26.9°C and 22-123mm, respectively). The experiments were run from March to May 2013. For a more detailed description of experimental sites see **(Farjalla *et al.* in prep)**. Dominant tank-bromeliad species at the three experimental sites were *Guzmania berteroniana, Vriesea splendens*, and *Neoregelia cruenta*, in Puerto Rico, French Guiana, and Macae, respectively.

Precipitation scenarios

Our aim was to simulate gradients of realistic precipitation scenarios that alter both the amount of rainfall entering bromeliads, and the frequency of rainfall events. We first determined the ambient rainfall distribution within each study site based on past rainfall data matching the period and length of experiments (*i.e.,* daily precipitation records from the past 5 to 10 years depending on study sites). We rounded rainfall amounts to integers and fitted a negative binomial distribution to the data for each site-year combination to estimate the mean (mu) and variance or dispersion (k) parameters for these distributions. The ambient rainfall distributions were then characterized by the averaged mu and k across all years and rescaled to mu = 1 and k = 1. From this ambient rainfall distributions (“mu1k1”), we generated gradients of increasing mu (ten parameters from mu = 0.1 to mu = 3) and k (three parameters from k = 0.5 to k = 2) parameters. Precipitation scenarios were thus factors relative to the unit values of mu and k. A total of thirty scenarios (10 mu x 3 k) were obtained where, for instance, the “mu0.1k0.5” scenario simulated a 90% decrease in the amount of water compared to “mu1k1” at half the frequency (on a negative binomial scale). We used a negative binomial distribution on each of the 30 scenarios to generate a 65-day rainfall schedule (rainfalls in mm) at each study site. This procedure was developed by **MacDonald and Srivastava (2013)** as part of a larger multi-site study. As rainfall events do not directly translate into a volume of water (in ml) collected by a plant in the understorey, we corrected values of the rainfall schedule by i) the mean catchment area of bromeliads obtained using image analysis and ii) the percentage of rainfall interception by canopy cover (**Trzcinski *et al.* under revision** in French Guiana for further details about correction factors).

Experimental design and data collection

Thirty medium-sized plants were selected (excluding juveniles and flowering plants), spaced at regular intervals from each other (~ 5 to 10 m), and placed under individual rain shelters with a cone-like shape and made of transparent plastic to prevent rainwater from entering the plant. Individual rain shelters were disposed ca. 80 cm above each bromeliad in a way to allow the air circulation and the movement of both terrestrial foragers and aquatic colonizers. Given the large number of replicates, the onset of the experiment was staggered in three temporal blocks. No significant effects of temporal blocks were detected in our statistical analyses; this variable was thus dropped from models in subsequent analyses. Since the composition and abundances of species in the aquatic community can vary among plants inducing a potential bias in the plant preference/selection by terrestrial organisms, we homogenized aquatic communities among plants at the beginning of the experiment. Three days before the experiment started, the aquatic invertebrates were collected using a 10-mL micropipette with the end trimmed to widen the aperture, identified, and returned to the 30 plants in equal proportions. Similarly, the fine organic matter was sampled, homogenized within a graduated cylinder, and the same quantity was distributed among plants to provide the aquatic invertebrates with nutrients. Then each plant was randomly assigned a precipitation scenario and watered daily according to the corrected rainfall schedule. We used rainwater filtered through a 500 µm sieves to water the plants. The main justification of this experimental design is that the gradient width of precipitation scenarios and geographical replication would compensate for the absence of replication per scenario within each site when trying to detect a terrestrial response.

During the 65-days experiment, the occurrence (*i.e.*, a proxy of abundance) and identity of all terrestrial species/morphospecies foraging or nesting on the leaves were recorded every day in the morning between 8:30 am and 12:00 am before watering the plants. Web-building spiders were also taken into account only if the web was, at least, partly attached to a bromeliad leaf. To avoid any observational biases, the same expert was designated within each study site to make observations throughout the experiment. Despite a turnover in species identity across regions this study targeted broad terrestrial taxonomic groups with contrasting morphological and behavioral attributes. These taxonomic groups had to be widely distributed (*e.g.*, present in at least 2 out of the 3 sites), easily identified (*e.g.*, Diptera were excluded), and directly linked to the bromeliad-dwelling aquatic community either preying upon emerging aquatic adults and/or nesting on bromeliad leaves. Three dominant terrestrial taxa were thus selected: spiders, ants, and frogs.

The water depth (WD) of two intermediate reservoirs (excluding the central reservoir and outermost senescent leaves) were measured daily and used to generate several variables describing the plant hydrology stability. The wetness index (Wi) was calculated as the mean WD divided by maximum WD. The water amplitude (Wa) was the difference between maximum WD and minimum WD. The water coefficient of variation (Wcv) is the ratio of standard deviation to the mean of WD. These variables were the averaged values of the two reservoirs. Another set of three complementary variables were generated using the corrected rainfall schedule and represent, to some extent, the effect of our presence/manipulation on the terrestrial organisms (intended rainfall). The total number of dry days (Dry) is a measure of the effect of our presence without watering/disturbing the plant. The total number of days a given plant overflows (Overflow) was calculated as the water volume this plant is expected to receive minus its maximum volume of water. The 'Overflow' is a measure of extreme disturbances. The last variable was the rainfall coefficient of variation (Rcv).

Finally, at the end of the experiment the maximum water volume of each plant (Vm *i.e.*, a proxy of the carrying capacity) was measured as the difference between a known volume of water added in an empty plant and the volume that overflows. Then, the total number of leaves (Nbl), and the plant width (Pw; the average of two measures of plant width taken at 90°) were recorded. This last set of variables represents descriptors of the plant morphological attributes, *i.e.*, proxies of habitat properties. Summary statistics of the selected ecological variables at the three study sites were provided in Table 1.

Statistical analysis

Spatial variations in selected ecological variables were investigated with multiple comparison tests based on Kruskal-Wallis rank sum tests using the R-package *pgirmess*. We then performed three distinct generalized linear models to evaluate the overall response of each terrestrial taxon (spiders, ants, and frogs) to selected ecological variables. In these models, the total occurrence of each taxon was used as response variable. The daily occurrence of each morphospecies *per* taxon was summed up *per* treatment/plant across all study period. We thus obtained the total spider, ant, or frog occurrence for each treatment/plant. Associated with each treatment/plant we included in our models the plant 'hydrological stability', 'morphological attributes', 'intended rainfall', 'country' (three level: PR, FG, M), and 'biotic interactions' with other taxa (either spider, ant, frog) as explanatory variables plus interaction terms. To avoid over-fitting of the data, models were built based on an *a priori* selection of ecologically relevant variables and interaction terms, as follows:

Log('Spider' + 1) ~ 'Hydrological stability' + 'Morphological attributes' + 'Intended Rainfall' + 'Country' + 'Ant occurrence' + 'Frog occurrence' + ' Two-way Interaction Terms'

Although the response variables were count data, our tests for goodness-of-fit of the models with chi-square tests based on the residual deviance and degrees of freedom indicate that a log transformation of the response variable with a Gaussian distribution was most appropriate. Note that in the model with ants as response variable, the 'country' had only two levels (FG and M) as ants were absent from Puerto Rico. A model selection based on the lowest AIC was performed using the R-package *MASS*. Once the final model was established, the significance of each term was assessed using Type-II tests, according to the principle of marginality, with the R-package *car*. Both significant and insignificant terms were kept in our final models. Only significant interaction terms from final models were used for visual representation using the R-package *visreg*.

To further determine the behavioral response of each dominant taxon to selected ecological variables while accounting for the temporal dynamic and country effect (knowledge gained from previous models see Result section), we used generalized linear mixed models (GLMMs) with each taxon's daily presence as response variable, and the daily presence of other taxa, the 'daily wetness index' and 'daily intended rainfall' plus interaction terms as fixed effects. Since terrestrial observations were performed early in the morning before we watered bromeliads, we impose a one-day lag in the daily intended rainfalls so the presence or absence of a given terrestrial species could be explained by an extreme watering event the day before the observation was made. Moreover, this latter variable was log-transformed to reduce its variability. The ‘plant ID’ nested within ‘country’ was specified as random effects. GLMMs with a binomial distribution were used as they provided the best fit to the data and met all statistical assumptions. Models were constructed as follows:

‘Daily Spider’ ~ ‘Daily Ant Presence’ + ‘Daily Frog Presence’ + ‘Daily Wetness Index’ + Log(‘Daily Intended Rainfall’ + 1) + ‘Two-way Interaction Terms’ + (1|Country/Bromeliad ID)

This model specification accounts for spatial and temporal autocorrelations among observations within a given treatment/plant at a given study location. Although previous models helped us understanding site-specific responses of arthropods and amphibians to broad environmental variables, this other set of models would provide complementary information on the strength of day-to-day responses to biotic interactions and our simulated precipitation treatments regardless of study location and plant morphological attributes. Finally, model selections for GLMMs were conducted using a multi-model averaging approach based on information criteria (AIC; using the R-package *MuMIn*). As the number of possible models grows exponentially with the number of predictors, model averaging could become computationally intensive, therefore this approach was not used in previous models (GLMs) as the number of predictors was high. This approach offers the opportunity to consider multiple models rather than focusing on a single ‘best’ one depending on the discrimination factor, a ΔAIC < 2 in this study. The relative variable importance (RVI), a measure of the importance of each explanatory variable, was calculated as the sum AIC weights of all best-performing models in which the variable of interest appeared. Adherences to model assumptions (homoscedasticity and model fit) were graphically assessed and Pearson residuals were plotted against each explanatory variable. All statistical analyses and figures in this study were generated using the R software version 3.2.1 **(R Core Team 2015)** and evaluated under a 95% confidence level.

RESULTS

Spatial variations in ecological variables

The characteristics of simulated rainfall events (‘intended rainfall’) in French Guiana and in Puerto Rico were not significantly different whereas the Macae site experienced a significantly higher number of dry days, bromeliads overflew significantly less often, and rainfall distribution was significantly more variable compared to FG's and PR's sites (Table 6.1, $P < 0.05$).

Table 6.1 Spatial variation in ecological variables (mean±SE, n = 30) throughout the study period. For each variable, study locations with different letters were significantly different (multiple comparison test following Kruskal-Wallis rank sum test, df = 2, P < 0.05).

	Study Locations		
	French Guiana	Macae	Puerto Rico
Rainfall distribution			
Number of dry days	26.9 ± 2.1^{a}	43.5 ± 1.3^{b}	23.3 ± 1.9^{a}
Number of overflow days	18.7 ± 2.1^{a}	1.4 ± 0.3^{b}	14.3 ± 1.8^{a}
Rainfall coefficient variation	2.0 ± 0.1^{a}	3.0 ± 0.1^{b}	1.8 ± 0.1^{a}
Habitat properties			
Maximum Volume	232.2 ± 10.9^{a}	1000.0 ± 22.1^{b}	354.8 ± 15.4^{c}
Number of leaves	14.2 ± 0.4^{a}	17.7 ± 0.5^{b}	24.5 ± 1.0^{c}
Plant diameter	71.7 ± 2.2^{a}	40.1 ± 0.8^{b}	79.8 ± 2.3^{a}
Hydrological stability			
Wetness index	0.7 ± 0.02^{a}	0.6 ± 0.03^{b}	0.6 ± 0.04^{b}
Amplitude	44.1 ± 2.2^{a}	75.9 ± 2.7^{b}	53.9 ± 2.1^{a}
Water coefficient variation	0.3 ± 0.02^{a}	$0.6 \pm 0.1^{a,b}$	0.6 ± 0.1^{b}
Taxa			
Spiders	13.8 ± 1.2^{a}	6.0 ± 1.3^{b}	26.7 ± 4.2^{a}
Ants	9.7 ± 1.8^{a}	6.1 ± 0.9^{a}	NA
Frogs	0.5 ± 0.2^{a}	0.4 ± 0.1^{a}	8.5 ± 1.3^{b}

Additionally, despite bromeliad species in the three study locations (*V. splendens*, *N. cruenta*, *G. berteroniana* in FG, M, and PR, respectively) had significantly contrasting morphological attributes (Table 6.1, $P < 0.05$), the plants in Macae and Puerto Rico displayed relatively similar hydrological stability. Hence, bromeliads in Macae had significantly larger maximum water volume ($V_m = 1000.0 \pm 22$ ml) compared to Puerto Rican bromeliads ($V_m = 354.8 \pm 15$ ml) and experienced two times the number of dry days than in Puerto Rico resulting in a similar wetness index of 0.6 ± 0.03 and 0.6 ± 0.04 for Macae and Puerto Rico, respectively (Table 6.1, $P > 0.05$). The wetness index of bromeliads in French Guiana was significantly the highest (0.7 ± 0.02). We noted some site-specific differences in the occurrences of the selected taxa among study locations. Spider occurrence was not significantly different between FG and PR. Ants occurred at equal frequencies in French Guiana and Macae but were never observed on bromeliads in Puerto Rico. Finally, Puerto Rican terrestrial assemblages were dominated by frogs (Table 6.1). Overall, French Guiana was the most species-rich site with 41 identified morphospecies (spider = 24, ants = 15, frogs = 2) and a total of 721 observations. By contrast, in Puerto Rico, four morphospecies of spiders and one of frog were identified for a total of 1054 observations. Finally Macae had only few morphospecies and a small number of observations per morphospecies (spiders = 2, ants = 1, frogs = 1, total number of observations = 377; Table 6.1).

Arthropod and amphibian responses to ecological variables

The relationship between the total occurrences of spiders and the wetness index was significantly influenced by the study location (LR $\chi^2 = 15.253$, P = 0.0005), the occurrence of frogs (LR $\chi^2 = 7.498$, P = 0.006), and to a lesser extent the occurrences of ants (LR $\chi^2 = 6.37$, P = 0.012, Table 6.2). For instance, spider occurrences increased with increasing wetness index values in FG and Puerto Rico whereas they decreased in Macae (Figure 6.1A). Additionally, spiders seem to preferentially colonize 'wet' plant when frogs are absent whereas they change their preferences to drier ones when amphibians are also present (Figure 6.1B).

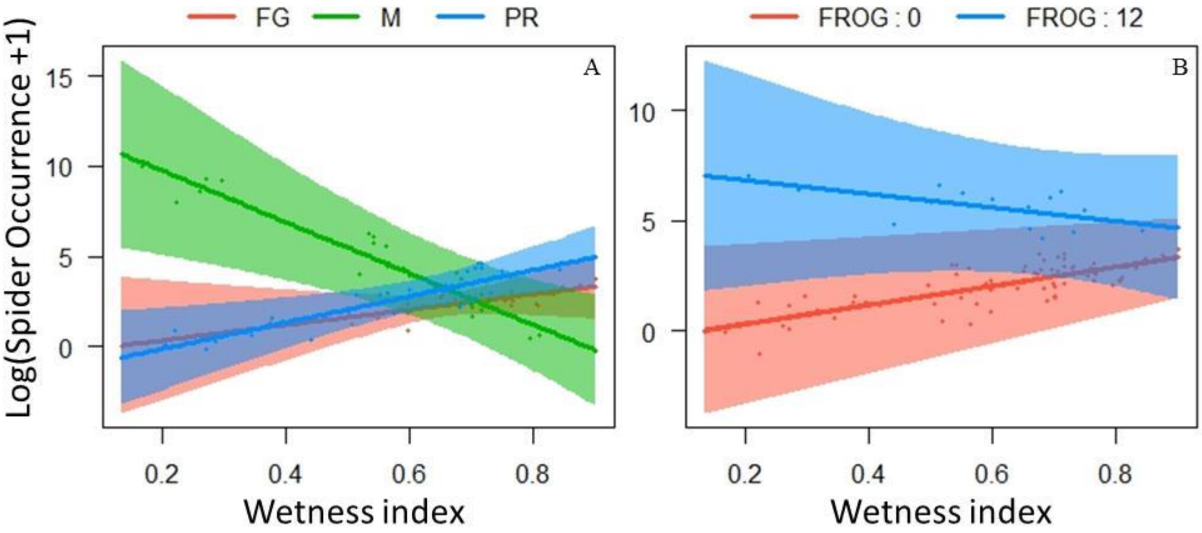

Figure 6.1 Graphs of the influence of significant interactions terms on the log-transformed occurrences of spiders. A) Wetness index:Country (FG = French Guiana; M = Macae; PR = Puerto Rico). B) Wetness index:Frog occurrences (Frog : 0, number of frogs = 0; Frog : 12, number of frogs = 12). Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians.

Table 6.2 Effects of the ecological variables on the total bromeliad-occupancy of the three dominant species (i.e., spiders, ants and frogs). Only final models with significant variables are shown. Note that response variables were log-transformed.

	LR χ^2	Df	P
Spider Occupancy			
Overflow	4.707	1	0.03
Vm	4.153	1	0.042
Wetness	0.921	1	0.337
Country	1.039	2	0.595
Ant	0.021	1	0.886
Frog	0.249	1	0.617
Country : Frog	7.478	2	0.024
Wetness : Country	15.253	2	0.0005
Wetness : Ant	6.37	1	0.012
Wetness : Frog	7.498	1	0.006
Ant Occupancy			
Dry	2.007	1	0.157
Vm	5.586	1	0.018
Country	3.538	1	0.06
Spider	0.589	1	0.443
Frog	0.182	1	0.67
Country : Frog	5.554	1	0.018
Dry : Country	5.496	1	0.019
Dry : Spider	5.54	1	0.019
Vm : Frog	6.588	1	0.01
Frog Occupancy			
Dry	1.538	1	0.215
Vm	0.094	1	0.759
Wetness	0.011	1	0.916
Country	35.514	2	1.942e-08
Spider	0.152	1	0.697
Country : Spider	15.757	2	0.0004
Wetness : Country	11.563	2	0.003
Dry : Wetness	4.344	1	0.037
Vm : Wetness	3.855	1	0.049
Wetness : Spider	7.674	1	0.006
Dry : Spider	8.404	1	0.004

Ants were significantly influenced by the occurrence of frogs, the maximum water volume, the study locations, and the total number of dry days in a complex way as shown by the significant interactions (Vmax:Frog, LR χ^2 = 6.588, P = 0.01; Country:Frog LR χ^2 = 5.554, P = 0.018; Dry:Country LR χ^2 = 5.496, P = 0.019; Table 6.2). Ants seem to avoid the larger plants in the presence of frogs (Figure 6.2A) and arthropods have opposite responses to frog occurrence in French Guiana and Macae (Figure 6.2B). Ants were not significantly influenced by variables related to the hydrological stability of the plant.

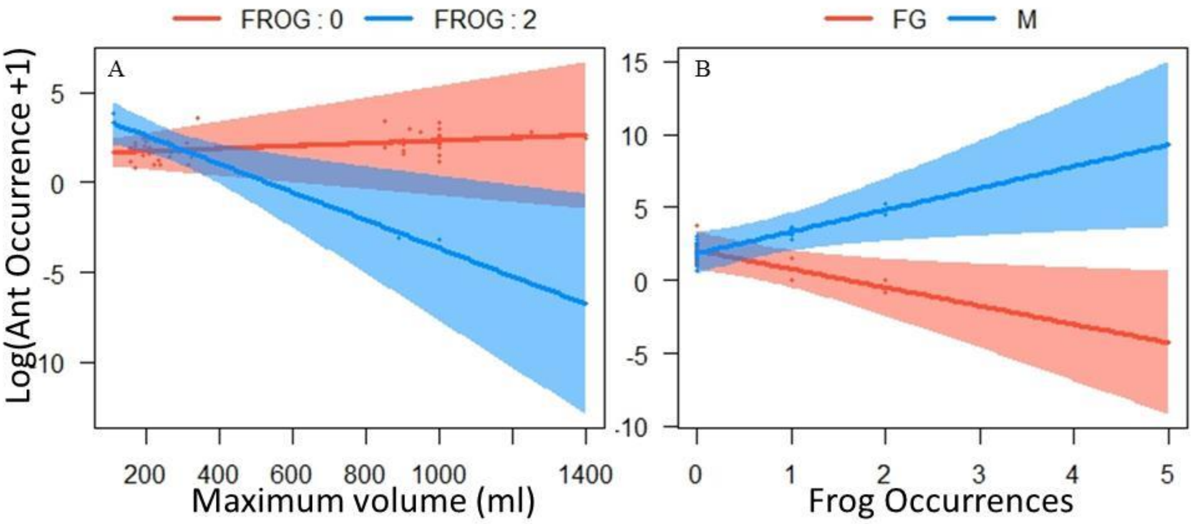

Figure 6.2 Graphs of the influence of significant interactions terms on the log-transformed occurrences of ants. A) Maximum water volume:Frog occurrences (Frog : 0, number of frogs = 0; Frog : 2, number of frogs = 2). B) Frog occurrences:Country (FG = French Guiana; M = Macae). Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians.

Frogs were significantly influenced by several ecological variables, which were included in interaction terms. The most influential variables were the interactions between the study locations and occurrence of spiders, as well as the wetness index (Country:Spiders, LR χ^2 = 15.757, P = 0.0004; Country:Wetness LR χ^2 = 11.563, P = 0.003; Table 6.2). Indeed, frogs were positively correlated with spider occurrence in French Guiana, negatively correlated in Macae and Puerto Rico, and preferred wet plants in FG and PR but not in Macae (Figure 6.3).

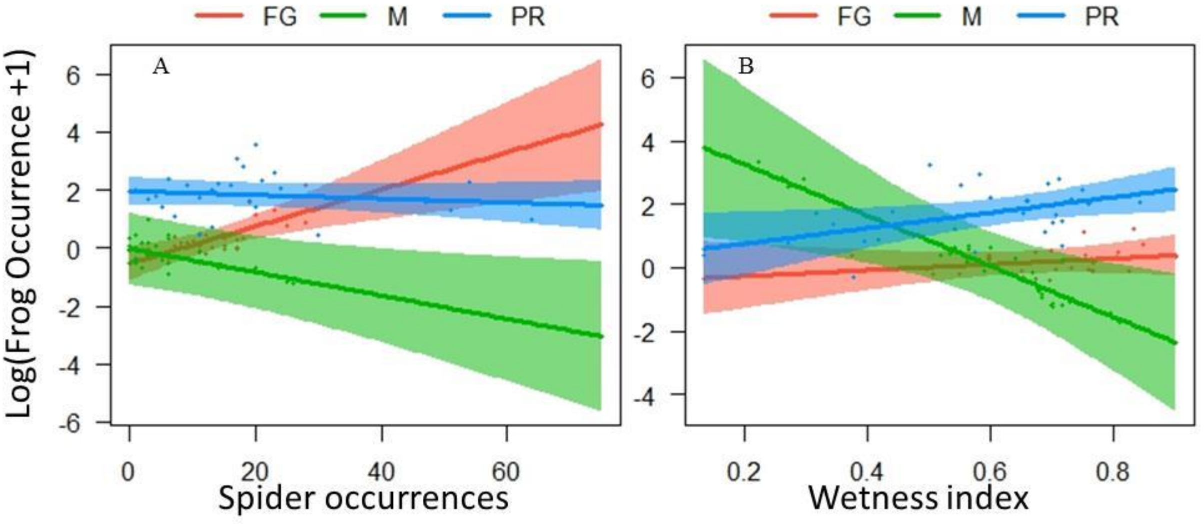

Figure 6.3 Graphs of the influence of significant interactions terms on the log-transformed occurrences of frogs. A) Spider occurrences:Country. B) Wetness index:Country (FG = French Guiana; M = Macae; PR = Puerto Rico). Shading represents 95% confidence intervals and points are partial residuals. Effects were plotted with additional variables held at their medians.

Overall, the study location, wetness index (*i.e.*, a proxy of hydrological stability), and biotic interactions with other taxa were the most influential variables on the total occurrences of spiders, frogs, and ants on bromeliads. Surprisingly, variables related to intended rainfall distributions had no to weak effects on arthropods and amphibians. Moreover we noted that ants showed moderate to weak sensitivity to changes in ecological variables compared to the other taxa (comparatively smaller likelihood ratio values and higher p-values).The daily presence of spiders on bromeliads was mostly influenced by the presence of frogs, and the wetness index (RVI = 0.24 and 0.17 for frogs and the wetness index respectively, Table 6.3).

Table 6.3 Effects of the ecological variables on the daily occurrence of each dominant guild as determined by model averaging from mixed-effect models. Each row corresponds to a single best-performing model. All models with the lowest AICs were considered equally important if ΔAIC < 2. The relative variable importance (RVI) is displayed in parentheses, along with model-averaged estimates (±SE), Z value, p-value, log-likelihood (logLik) and Akaike metrics.

	Estimate ± SE	Z Value	P	logLik	ΔAIC	w
Spider Occurrence						
Intercept	-0.99 ± 0.94	1.047	0.295	-2198.9	0.0	0.31
Frog Occurrence (0.24)	0.04 ± 0.1	0.346	0.729	-2198.5	1.19	0.17
Wetness (0.17)	-0.02 ± 0.09	0.173	0.863	-2198.8	1.8	0.13
Ant Occurrence (0.16)	0.002 ± 0.06	0.038	0.970	-2198.9	1.99	0.11
Ant Occurrence						
Intercept	-1.24 ± 1.13	1.098	0.272	-1188.4	0.0	0.45
Wetness (0.21)	0.05 ± 0.18	0.274	0.784	-1188.2	1.52	0.21
Frog Occurrence (0.17)	0.03 ± 0.26	0.118	0.906	-1188.4	1.92	0.17
Spider Occurrence (0.17)	0.005 ± 0.06	0.078	0.938	-1188.4	1.96	0.17
Frog Occurrence						
Intercept	-2.6 ± 2.31	1.126	0.260	1574.7	0.0	0.42
Spider Occurrence (0.25)	0.04 ± 0.11	0.377	0.706	1575.8	1.05	0.25
Wetness (0.18)	0.03 ± 0.13	0.200	0.841	1576.5	1.73	0.18
Ant Occurrence (0.16)	0.03 ± 0.21	0.142	0.887	1576.6	1.90	0.16

The daily presence of ants was mainly influenced by the wetness index (RVI = 0.25) while frog presence responded to the presence of spiders and the wetness index (RVI = 0.25 and 0.17, respectively). Conversely, the effect of daily precipitations experienced by each taxon was consistently not detected in the best-performing models. Overall, the presence of spiders, ants, and frogs on bromeliads through time was influenced by biotic interactions with each other as well as the hydrological stability of the plant represented by the wetness index. The model-averaging method selected three best-performing models (ΔAIC < 2) with a single explanatory variable for each response variable. Although the model-averaged coefficients were not significant, these best-performing models were still able to detect a signal of the hydrological stability and biotic interactions as highlighted in previous models (GLMs) on the total occurrences of each taxon, suggesting an overall strong influence of these variables.

DISCUSSION

Effects of precipitation scenarios across the biogeographic gradient: contingency in the response of dominant taxa

This study is innovative in using a consistent methodology to simulate precipitation change scenarios across a biogeographic gradient of environmental conditions and species pools, thus providing causal inferences about the generality of biological responses to climate change. As expected, study locations induced some variability in the direction and magnitude of the response of dominant taxa to precipitation scenarios. This context-dependence in the response can be explained by two potentially synergistic processes. First, study locations display contrasting environmental conditions, and precipitation records indicate that Macae was the driest of all sites whereas Puerto Rico and French Guiana were wetter and comparatively more similar. Second, sites differ in species richness, species identities, and functional traits within each taxonomic group. Together, drier conditions in Macae, in addition to a depauperate species pool, resulted in an increased magnitude of the terrestrial response to hydrological stability as proxied by the wetness index (Figure 6.1A and Figure 6.3B). It is thus likely that effects of our precipitation gradient were exacerbated in drier sites. Assuming that i) the species pool in Macae is adapted to dry conditions, ii) spiders and frogs tend to escape wet scenarios (this study), and iii) the south eastern coasts in south America are predicted to become wetter **(Magrin *et al.* 2014)**, we expect Brazilian bromeliads to be adversely impacted by future precipitation scenarios in the area. Conversely, high species richness is known to confer some stability at community-wide levels through a portfolio effect where a diversified set of species are differentially sensitive to various environmental factors **(Schindler *et al.* 2015)**. French Guiana was the richest and the wettest of all sites, we thus assumed it may benefit from this portfolio effect when facing extreme precipitation events (in either dry or wet scenarios). Puerto Rican bromeliads hosted distinct terrestrial taxa where we noted the absence of ants, and where despite reduced frog and spider richness, these latter species occurred at higher frequencies than in French Guiana. Occurrences in this study are close proxies of the relative abundance of morphospecies. The sites in French Guiana and Puerto Rico displayed similarly low variability (*e.g.,* smaller confidence interval in Figure 6.1A and Figure 6.3B) in the response of spiders and frogs to our treatments despite contrasting underlying mechanisms: higher species richness and evenly distributed occurrences per species in the former country and a few numerically dominant species in the latter country. Hence, if these dominant species in Puerto Rico converge in their sensitivity to future climatic scenarios, we expect the Puerto Rican communities to experience a drastic collapse in ecosystem functioning compared to those in French Guiana.

Effects of hydrological stability and interspecific interactions: generality in the response of dominant taxa

One of our most consistent results, regardless of study locations, is that precipitation scenarios proxied by the intended rainfall had no to little effect on the site-selection by terrestrial organisms. Instead, these organisms rather recurrently tracked changes in hydrological stability, which resulted from a complex interaction between simulated rainfall distributions and habitat properties (maximum water volume). Likewise, **Brendonck et al. (2015)** found that hydrological stability was a crucial determinant of community assembly in temporary aquatic systems. In this study we found that spiders changed their preference for a given level of wetness when frogs were also present (Figure 6.1B). Some authors predict the strength of biotic interactions to weaken as habitat stability decreases **(Wellborn *et al.* 1996)** whereas others found unanticipated consequences on decomposition rates via the cascading effect of biotic interactions **(Marino *et al.* in prep)**. We may not be able to ascertain the relationship between hydrological stability and biotic interactions in this study, but our results add to the evidence that these two ecological variables play a crucial role in the response of both aquatic and terrestrial communities to climate-driven disturbances. Importantly, this response is likely to be a general feature of ecological communities as it was consistently detected in our models.

Frogs and spiders displayed a strong mutual influence whose magnitude was biased in favor of frogs whereas the sign of the relationship depended on the study location (Table 6.2, Figure 6.1 and 6.3) supposedly due to a turnover in species composition for both taxonomic groups. Hence, frogs and spiders may be linked by antagonistic interactions where they either prey on each other or compete for a shared resource (nesting site and/or preference for a given prey). Abundance is often assumed to be an accurate proxy of the functional importance of species within the community **(Whittaker 1965, Grime 1998)**. Despite low occurrences/abundances, our models consistently detected the influence of frogs on other species suggesting that biomass in this case would implicitly be a better proxy of the functional importance of frogs. By contrast, ants seem to show no to weakly significant influence by either biotic or abiotic conditions. First, individuals of some ant species were found to forage on bromeliad leaves probably seeking for food, therefore their occurrence were likely to be influenced by antagonistic interaction with other members (frogs and/or spiders) or by other environmental variables as detected by our models. However, most of the time ant colonies settled in a given plant thus being robust as a colony to external disturbances (depending on ant colony size; **Barbieri *et al.* 2015**). We purposely focused on total and daily occurrences to overcome issues related to interspecific variations in abundances/biomasses among taxa. In this sense, an ant colony or a single web-building spider staying several successive days on a given plant were given similar weights in our models. Altogether the results of this study suggest that in a context of environmental changes, the abiotic niche of species in which their fitness is optimized, may be modified or constrained by fluctuations in the biotic niche.

Where shall we go from here?

Our gradient of precipitation encompasses a 30-fold increase in the amount of water from the dry to wet scenario while frequency between the two extreme treatments varied by a factor of 4. Despite conspicuous width in the precipitation gradient, diverse animal species were more sensitive to the hydrological stability of the system itself, which strongly buffered variations in rainfall patterns. Indeed, the wetness index was above a value of 0.5 in all countries where a value falling below 0.5 would indicate more sensitivity to changes in precipitation schemes. The plant's morphological properties thus buffered temporal variations in precipitations resulting in relatively stable hydrological dynamics. These results corroborate those found by **Dézerald et al. (2015a)**, where the distribution of abundance-weighted traits of aquatic invertebrate communities in bromeliads remained almost constant under a simulated drought that corresponded to three times the maximum number of consecutive days without rainfall under ambient climate. A recurrent question in experimental ecology is to what extent a system should be disturbed to pinpoint an ecological response. Our approach indicates that species started to show a marked response in extreme scenarios (either dry or wet), we thus encourage future studies to stretch gradients of ecological variables to clearly highlight thresholds in species responses. Although the duration of our experiment matches the timeframe of behavioral responses to precipitations, greater understanding of species-disturbance relationships would also be gained by matching the length of experiments to the timeframe of physiological response of species as in long-term studies **(Woodward *et al.* 2012)**.

Finally, predicting the effect of global environmental changes on multi-trophic communities is challenging as not all species are directly and synchronously impacted by a given disturbance, but potentially via the multiple chains of indirect effects **(Harrington *et al.***

1999, Newman 2004, Pritchard *et al.* 2007, Barton & Ives 2014). For instance, spiders have been found to enhance leaf-litter decomposition rates in dry precipitation scenarios by preventing overgrazing of fungi by Collembolla (**Lensing & Wise 2006**, see also **Johnson *et al.* 2011**). Also, in our experiment, we focused on one aspect of global environmental changes: precipitation. As amphibians are threatened by multiple factors **(Becker & Zamudio 2011)** we could assume bromeliad-dwelling spiders to be released from antagonistic interaction with frogs, potentially leading to increased predation rates on aquatic insect emergence (from the bromeliad tanks) by spiders and ultimately affecting ecosystem-wide functions. Large-scale experiments, as illustrated here, allow reaching unprecedented level of complexity in our understanding of environmental-driven changes in ecosystem-wide functioning but paradoxically confidence in our predictions also decreases with increasing ecological complexity (*e.g.,* via increasing the number of potential outcomes following a given disturbance). Therefore, accumulating knowledge of environmental factors that are most influencing to species and their functional role is the first step in attempting to accurately predict the ecological effect of climate-driven changes.

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DISCUSSION

On peut réellement connaître le fonctionnement d'un système dès le moment où on entrevoit les limites à partir desquelles il fonctionne différemment ou plus du tout. Eu égard à la nature des changements environnementaux considérés et des protocoles expérimentaux utilisés au cours de cette thèse, les limites de « l'écosystème broméliacée » n'ont pas été franchies. Le point fort de cette thèse est d'étudier un même modèle, en combinant différentes échelles biotiques, spatiales, et temporelles, en utilisant des données empiriques obtenues à partir de manipulations expérimentales permettant de déterminer la réponse des communautés à l'hétérogénéité naturelle des habitats et à des changements drastiques de conditions environnementales.

L'ensemble de nos résultats provenant de différentes échelles spatiales et d'approches (observations et expérimentations) convergent vers l'idée d'une certaine stabilité des communautés d'invertébrés face à une augmentation des températures, à une sécheresse locale, et à différents scénarios de précipitation. Cette stabilité est conférée par les caractéristiques physiques de l'habitat (traits végétatifs de la plante à réservoirs), par les traits de résistance des espèces d'invertébrés aquatiques, et par la ségrégation spatio-temporelle des niches des espèces. Une fonction écosystémique principale, telle que la décomposition, reste assurée par un cœur densément connecté de détritivores et de micro-organismes, présent sur l'ensemble de l'aire de distribution des broméliacées à réservoirs, et continuellement alimenté par la chute de litière et de cadavres d'organismes terrestres. Une importante quantité de matière, composée essentiellement de diptères et de coléoptères, est ensuite exportée vers le milieu terrestre au bénéfice de taxons gravitants autour des broméliacées. Ces caractéristiques générales démontrent que la dynamique de ces écosystèmes miniatures est stable et que leur fonctionnement est étroitement connecté à la matrice terrestre environnante.

1 Structure des réseaux trophiques et fonctionnement du système face à l'hétérogénéité naturelle des facteurs biotiques et abiotiques

Quelles que soient les échelles d'étude prises en compte, biotique, spatiale, et temporelle, certains facteurs comme le volume d'eau, la présence de prédateurs, et l'exposition à la lumière via une modification du couvert végétal ont une influence sur la structure et le fonctionnement des communautés aquatiques des broméliacées à réservoirs.

1.1 Capacité d’accueil du système: le volume d’eau

Le volume d’eau contenu au creux des feuilles des broméliacées est bien souvent considéré comme un proxy de la taille de l’habitat et de la capacité de charge du milieu. En ce sens, la richesse spécifique des broméliacées confirme les prédictions de la relation aire-espèce qui prédit une corrélation positive entre la richesse spécifique et la surface ou le volume disponible pour la colonisation. Bien que largement reconnue pour ce système, cette corrélation est confirmée par nos résultats concernant la structure des réseaux trophiques (Chapitre 2), avec une augmentation de la richesse spécifique et de la densité de liens avec le volume d’eau. Le volume d’eau filtre l’entrée dans le système de groupes taxonomiques particuliers **(Amundrud & Srivastava 2015)**. En effet, les top prédateurs, comme les larves d’odonates et de diptères (Tabanidae, Culicidae) sont présents en abondance dans les grosses broméliacées *Aechmea aquilega* des milieux ouverts (Chapitre 2) alors qu’elles sont rares voire absentes des petites *Vriesea splendens* de milieux forestiers (Chapitre 1 et 2). Cependant, nos résultats ne peuvent pas discriminer avec certitude l’influence relative des variations des volumes d’eau et de la structure du couvert végétal.

Les taxons dont le mode de dispersion est passif via la phorésie comme les ostracodes et les oligochètes sont aussi exclus des plus petits réservoirs (Chapitre 1). Un constat évident si l’on considère le comportement d’oviposition des amphibiens sélectionnant des habitats de plus grand taille et moins sensibles aux évènements de sécheresse **(Poelman *et al.* 2013)**. La grande majorité des taxons restants peuvent venir coloniser jusqu’au plus petit des volumes d’eau dans des plantes ayant tout juste mis en place les premiers réservoirs, soit quelques millilitres.

1.2 Le rôle des prédateurs à l’apex du réseau trophique

Le rôle des prédateurs à l’apex du réseau trophique est considéré comme prépondérant sur la structure et le fonctionnement de ce système. Bien que leur entrée dans le système soit en partie déterminée par le volume d’eau, leur présence diminue significativement la densité de liens et l’emboîtement, conduisant à une structure organisée de façon non aléatoire (Chapitre 2). Ces résultats confirment ainsi les analyses théoriques de la structure des réseaux trophiques **(McCann 2000, Allesina & Tang 2012)**. A une échelle spatiale fine, au sein d’une plante, un prédateur au dernier stade larvaire comme *Toxorhynchites haemorrhoidalis* peut effectivement consommer jusqu’à 400 larves de moustiques sur la durée du dernier stade larvaire (< 1 mois, Chapitre 4) ayant un impact drastique sur la dynamique des populations de ses proies. En revanche, certains facteurs limitent l’influence de la prédation sur la communauté. Nous avons vu que les petits volumes d'eau constituent des refuges à la prédation. Certaines proies (Culicidae) peuvent atteindre des classes de tailles refuges à partir desquelles les contraintes mécaniques sont trop importantes pour les prédateurs comme *Corethrella* sp. et Tanypodinae sp. (Chapitre 1). Certains Culicidae ont mis en place des comportements d'évitement à travers une baisse de leur activité de recherche de nourriture en présence de larves d'odonates **(Hammill *et al.* 2015)**. D'autres proies ont aussi acquis des traits de résistance à la prédation comme les fourreaux des trichoptères au Costa Rica (Chapitre 3) ou alors les valves calcaires des ostracodes (Chapitre 1). Nous avons aussi démontré que la pression de prédation sur une proie aquatique était atténuée par l'attraction préférentielle du prédateur *T. haemorrhoidalis* pour une proie terrestre (Chapitre 4).

1.3 Importance du couvert végétal et de l'exposition à la lumière

La quantité de lumière incidente est une mesure directe de l'ouverture du milieu (énergie incidente pour la production primaire) et indirecte de la quantité de litière entrante dans les réservoirs. En ce sens, le rayonnement incident pourrait avoir un impact indirect sur les communautés d'invertébrés aquatiques via la modification des effets ascendants. De prime abord, la quantité de matière organique détritique (*e.g.,* feuilles mortes, brindilles, graines en décomposition) à la base du système ne semble pas limitante quel que soit le degré d'ouverture du milieu **(Richardson *et al.* 2000a, Armbruster *et al.* 2002)**. Cependant, une étude récente a mis en évidence l'importance d'une ressource non détritique que sont les algues **(Brouard *et al.* 2012)**. Celles-ci sont présentes en plus grande abondance dans les plantes exposées à la lumière par rapport à celles situées dans un milieu fermé. L'utilisation des outils isotopiques suggère que le degré de dépendance des invertébrés aquatiques au carbone issu de litière en décomposition ou provenant d'algues dépend du ratio des deux ressources dans le système, un résultat observé sur un large gradient latitudinale en Amérique latine **(Farjalla *et al.* en prép)**. Comparées à la matière organique détritique, les algues sont une nourriture de meilleure qualité, riche en acides gras polyinsaturés, dont l'ensemble du réseau trophique peut bénéficier. Ce dernier aspect justifie alors l'utilisation des approches stœchiométriques pour des études futures sur l'influence de la ressource à la base des chaînes alimentaires.

La structure du couvert végétal et la quantité de lumière incidente semblent indirectement modifier le fonctionnement des communautés via la ressource à la base du réseau mais pourraient aussi directement influencer les invertébrés aquatiques. En effet, on observe un remplacement parfois complet de la composition spécifique de certains groupes fonctionnels entre ces deux milieux. Conjointement à ces observations, l'exposition lumineuse sélectionne les espèces de broméliacées avec des caractéristiques morphologiques contrastées (volume d'eau, nombre de réservoirs disponibles, Chapitre 1). Ainsi, certaines espèces comme *V. splendens* se retrouvent en milieu forestier alors que d'autres comme *A. aquilega* préfèrent les milieux ouverts. A notre connaissance il n'existe pas d'association entre l'espèce de broméliacée et les invertébrés aquatiques **(Jabiol *et al.* 2009)**. Le filtrage environnemental via la lumière et/ou les caractéristiques de la matrice terrestre environnante se ferait alors potentiellement sur les stades adultes. Finalement, l'influence du rayonnement incident est observée d'une échelle régionale à biogéographique soulignant l'importance de ce facteur dans le fonctionnement des communautés de broméliacées à réservoirs (Chapitres 2 et 3).

1.4 Réponse des communautés aux fluctuations saisonnières naturelles

L'influence des fluctuations naturelles de l'environnement sur les communautés tropicales et celles des broméliacées à réservoirs en particulier était jusqu'à présent rarement étudiée. Pourtant l'influence des cycles saisonniers sur les communautés terrestres et aquatiques des climats tempérés sont bien reconnus. En milieu tropical ces cycles sont atténués pour laisser place, grossièrement, à deux saisons en ce qui concerne la Guyane Française: une saison sèche d'août à novembre et une saison humide le reste de l'année, avec une réduction des précipitations au mois de mars. Les fluctuations de températures sont corrélées négativement à celles des précipitations et oscillent entre 19°C et 33°C pour une valeur moyenne de 24.5°C et des valeurs maximales de plus de 45°C. Cependant, sur l'année, la dynamique des populations était très faiblement influencée par ces fluctuations abiotiques, excepté quelques espèces sensibles à la température (Chapitre 1). **Richardson et al. (2015)** ont aussi démontré pour une période de 12 ans que les abondances et fréquences de certains organismes aquatiques étaient stables. Au sein d'une communauté de 22 espèces, les 11 espèces que nous avons étudiées, ont été trouvées tout au long de l'année, constamment exportées vers le milieu terrestre, et représentaient 90% de la biomasse moyenne annuelle.

A l'échelle de la plante, cet export peut être considéré comme une perte de nutriments qui est régulé et maintenu dans le système via les prédateurs comme les odonates **(Ngai & Srivastava 2006)**. Mais à l'échelle de la population de plantes, ces organismes en retournant pondre dans les réservoirs d'eau, réinjectent une partie de cet azote dans le système. Cette organisation en métacommunauté crée une dynamique complexe permettant à un ensemble d'espèces d'exister et de cohabiter temporellement et spatialement. Ce système est donc intrinsèquement connecté à la matrice terrestre environnante **(Romero & Srivastava 2010)** et ce fonctionnement est quasi indépendant des fluctuations saisonnières. Si le compartiment aquatique est largement étudié, son influence sur la partie terrestre l'est beaucoup moins. D'un point de vue holistique cette dépendance à la matrice terrestre s'évalue en comparant la productivité d'un milieu donné par rapport à la productivité de la matrice environnante. On peut alors se demander à quel point les caractéristiques physiques d'un écosystème (taille, caractéristiques des lisières, ratios du volume sur la surface d'échange) modulent les flux d'énergies entre écosystèmes adjacents? **Gratton and Vander Zanden (2009)** présentent une intéressante synthèse bibliographique sur le sujet mais ne prennent pas en compte les écosystèmes miniatures.

2 Stabilité des écosystèmes face à certains aspects des changements environnementaux

Manipuler expérimentalement certains facteurs environnementaux, et décrire leurs conséquences sur les communautés écologiques, permet d'améliorer notre compréhension du fonctionnement de ces systèmes et d'affiner nos prédictions sur l'impact des changements futurs.

2.1 Effets tampons liés aux caractéristiques physiques de l'habitat et aux traits de résistance à la dessiccation des organismes

Une modification des conditions environnementales n'entraîne pas une réponse immédiate des communautés écologiques. Ce constat est particulièrement évident pour les milieux aquatiques **(Bond *et al.* 2008, Lake 2011, Sim *et al.* 2013, Brendonck *et al.* 2015)** où des changements de régimes de précipitions n'affectent pas directement l'hydrologie des systèmes. Dans les écosystèmes d'eau douce, l'hydrologie est définie comme le mouvement et la qualité des masses d'eau. Les caractéristiques morphologiques et la complexité (nombre de feuilles divisant le volume d'eau) des broméliacées assurent une bonne rétention de l'eau au creux des réservoirs, donc une bonne résistance à l'arrêt des précipitations sur plusieurs semaines (Chapitre 5). Les organismes sont d'ailleurs plus sensibles à l'hydrologie du système qu'aux variations des précipitations et cela indépendamment de la localité biogéographique (Chapitre 6). De la même manière, **Marino *et al.* (en prép)** ont démontré que, chez de nombreux diptères, le risque de prédation est moins important que la probabilité d'assèchement de cet habitat, dans le processus décisionnel conduisant à la sélection du site d'oviposition.

Cet effet tampon via les caractéristiques morphologiques de la plante hôte est renforcé par les traits de résistance à la dessiccation (œufs de résistance, temps de génération court, Chapitre 1 et 5) des organismes aquatiques. Ces traits ont été très largement documentés chez des organismes des milieux aquatiques temporaires des climats tempérés **(Reznickova *et al.* 2007, Céréghino *et al.* 2012)**. Leur présence chez des organismes tropicaux souligne l'importance des phénomènes climatiques extrêmes, qui diffèrent de la fluctuation environnementale naturelle, dans la sélection du groupe d'espèces des broméliacées à réservoirs. Un autre facteur qui influence potentiellement les organismes aquatiques lors d'assèchements est une augmentation de la température de l'eau. Mais là encore nos résultats démontrent qu'un prédateur à l'apex du réseau est résistant à des variations allant de 25°C à 33°C (Chapitre 4), et sans doute bien au-delà puisque des larves de *Toxorhynchites* sp. ont été trouvés dans des broméliacées exposées à des températures ambiantes supérieures à 40°C (observations personnelles). Les caractéristiques morphologiques de la plante hôte et les traits fonctionnels des espèces contribuent ainsi à la résistance des communautés des broméliacées à réservoirs aux fluctuations environnementales. Finalement, la structure du couvert végétal pourrait aussi jouer un rôle dans l'atténuation des fluctuations environnementales.

2.2 Une résilience rapide mais dépendante des caractéristiques de la perturbation

Suivant l'arrêt d'une perturbation ou d'un changement des conditions environnementales, les communautés peuvent retourner à leur état d'origine, on parlera de résilience, ou s'engager dans un fonctionnement différent, on parlera alors de phénomène d'hystérésis ou d'état alternatif **(Scheffer *et al.* 2001)**. Nos travaux montrent une résilience des communautés suivant le retour d'un régime normal des précipitations (Chapitre 5). Bien que la sécheresse appliquée dans cette expérience soit très localisée et sur une fraction seulement des îles que constituent les broméliacées d'une forêt, ces résultats soulignent deux points importants concernant l'effet d'une perturbation sur la résilience des communautés. Premièrement, l'effet d'une perturbation à l'échelle du paysage est hétérogène puisque, par exemple, la mortalité des arbres dans une forêt due à la sécheresse est différentielle **(Breshears *et al.* 2005)**. Similairement, l'assèchement des broméliacées était variable malgré nos efforts pour sélectionner des plantes avec des caractéristiques morphologiques comparables (Chapitre 5). Cet assèchement différentiel crée ainsi une mosaïque hétérogène d'habitats refuges. Avec l'intensification de la perturbation, cette mosaïque s'homogénéise pour ne donner que des habitats impactés. Deuxièmement, les capacités de dispersion/colonisation des espèces, en fonction de la densité d'habitats refuges et indirectement de la durée/intensité des perturbations, vont déterminer la vitesse de résilience. En ce sens, la résistance et la résilience d'une communauté est à appréhender en regard des caractéristiques de la perturbation appliquée (intensité, durée, et fréquence).

2.3 Une coexistence favorisée par la ségrégation spatiale de l'utilisation des ressources

Nos résultats ont permis de définir trois catégories d'organismes (Chapitre 1). Ceux présents toute l'année et dont les densités sont constantes, ceux présents toute l'année mais dont les densités montrent un ou plusieurs pics, et les espèces rares pour lesquelles on a retrouvé seulement quelques individus. Quels mécanismes expliquent de tels patrons de fluctuation des densités ? Dans ces écosystèmes miniatures, la compétition est si forte qu'elle a conduit sans doute à l'exploitation différentielle des ressources disponibles et à la ségrégation des niches des quatre espèces de la première catégorie (*Cyphon* sp., *Corethrella* sp., *Trentepohlia* sp., et *Elpidium* sp.).

Cette partition des ressources peut être d'ordre spatial. Par exemple, deux espèces phylogénétiquement proches comme *Microculex stonei* et *Wyeomyia* spp. (Culicidae) appartiennent toutes deux au groupe fonctionnel des filtreurs, mais la première filtre la matière en suspension dans la colonne d'eau et celle proche de la surface alors que la seconde filtre la matière fine qui sédimente au fond des réservoirs (**Clements 1992**, observations personnelles). Le partitionnement spatial des ressources est un phénomène couramment observé dans le règne animal, chez les fourmis **(Albrecht & Gotelli 2001)**, les oiseaux **(Bocher *et al.* 2014)**, et les mammifères **(Johnson & Franklin 1994)** par exemple. Cette stratégie différentielle d'acquisition de l'énergie se retrouve aussi chez les prédateurs principaux comme les larves d'odonates présentes sur la partie supérieure des feuilles et les larves de diptères Tabanidae présentes à la base des feuilles au fond des réservoirs (observations personnelles). Cependant, à plus large échelle spatiale, nos données non publiées montrent que ces deux prédateurs coexistent rarement localement mais lorsqu'ils cohabitent, ils occupent des niches différentes. Nos résultats ne peuvent alors certifier si ce patron de coexistence est la résultante d'un filtrage environnemental sur les adultes terrestres et/ou la compétition aux stades larvaires.

2.4 Une coexistence favorisée par la ségrégation temporelle de l'utilisation des ressources

La partition des ressources peut aussi s'effectuer dans le temps comme pour les espèces de la deuxième catégorie. Ceratopogonidae sp.1 et Orthocladinae sp., par exemple, ont des pics de densité décalés dans le temps, et ce patron est aussi observé pour deux espèces du même genre, *W. aphobema* et *W. lamellata* (Figure B2 et Figure B3 du Chapitre 1) même si toutes ces espèces cohabitent tout au long de l'année. Tout comme la ségrégation spatiale de l'utilisation des ressources, le partitionnement temporel de la distribution des espèces est observé chez d'autres organismes comme les fourmis **(Houadria *et al.* 2015)**. Cette variabilité des densités annuelles est potentiellement due à une augmentation de la température pour ces dernières espèces comme indiqué par les résultats du Chapitre 1. L'influence de la prédation serait un mécanisme potentiel mais il est à exclure ou du moins son influence est négligeable sur les organismes de la première catégorie pour des raisons de contraintes mécaniques. Son influence est aussi négligeable mais possible sur les jeunes stades (avant d'avoir atteint une taille refuge) des proies de la seconde catégorie. Son influence est cependant grande sur les oligochètes, dont nous n'avons pas déterminé les fluctuations de densités, mais qui représentent à eux seuls une part non négligeable de la biomasse annuelle. Dans tous les cas les espèces de ce système sont susceptibles de suivre les changements de différents facteurs environnementaux (biotique et/ou abiotique) d'après l'effet portfolio. Il serait donc intéressant de vérifier si les patrons de ségrégation temporelle observés dans ce Chapitre 1 se répètent les années suivantes ou si ces pics de densité reflètent simplement la variation locale et rapide d'un facteur que l'on n'aurait pas pris en compte.

2.5 Un seuil de basculement fonctionnel difficile à franchir

Entrevoir les limites du fonctionnement d'un système permet de mieux le connaître. Les limites du système broméliacées ont été approchées mais pas atteintes. Nous avons certes atteint un seuil de basculement du fonctionnement de la communauté en provoquant une sécheresse prolongée (Chapitre 5) mais pas suffisant pour induire un changement irréversible de son fonctionnement. Après une diminution de 90% du volume d'eau, la communauté n'était représentée que par les Culicidae filtreurs, le fonctionnement du système (*e.g.*, décomposition de la matière grossière par les déchiqueteurs ou l'ingestion du biofilm bactérien par les brouteurs) étant ainsi ralenti par l'absence des autres groupes fonctionnels. Les groupes fonctionnels correspondant aux déchiqueteurs et aux brouteurs présentent une faible richesse spécifique avec une et deux espèces respectivement contre quatre espèces chez les filtreurs. La présence de tous les traits fonctionnels dans le système jusqu'à une baisse de 90% du volume d'eau suscite alors la question de l'importance de la redondance fonctionnelle dans ce système.

D'après l'étude des propriétés topologiques des réseaux trophiques (Chapitre 2), la stabilité de ces derniers semblerait plus grande en milieux ouverts qu'en milieux fermés.

Toutefois, les Chapitres 1 et 5 semblent indiquer que les communautés aquatiques des plantes en milieux fermés sont aussi stables face à certaines perturbations. En appliquant une sécheresse similaire, la communauté aquatique serait-elle plus stable si elle est densément connectée, dans des volumes d'eau importants, en milieux ouverts propices à la sécheresse, ou moins connectée, dans de plus petits volumes, dans des zones de bas-fonds moins soumises à cette sécheresse? A quel point les seuils de basculement varient entre ces deux milieux sachant qu'il y a un remplacement des espèces au sein des groupes fonctionnels, notamment chez les prédateurs? Cette dernière question suppose que la diminution du volume disponible augmente les taux de rencontres entre proies et prédateurs et donc exacerbe l'effet de la pression de prédation. Si les résultats de ces travaux ne peuvent répondre à de telles questions, on peut tout de même supposer que ces communautés aquatiques dans différents milieux sont stables et adaptées à un régime de fluctuations naturelles et que seuls des évènements climatiques extrêmes pourraient modifier drastiquement le fonctionnement du système. Ultimement, si chaque organisme présente un seuil de basculement différent en réponse à une perturbation on peut alors se demander à quel point le seuil critique de la communauté aquatique est proche de celui de la plante hôte? En d'autres termes, pour un épisode de sécheresse donné, la communauté aquatique sera impactée à partir d'une baisse significative du volume d'eau, mais si cet évènement perdure, le métabolisme et le développement de la plante hôte mutualiste seraient perturbés et sa survie menacée.

3 Quelles échelles d'étude pour quels patrons de diversité?

Chaque communauté est unique dans l'espace et dans le temps **(MacArthur 1984 dans Roughgarden 2009)**. La communauté symbolise le barreau intermédiaire sur l'échelle biotique qui va des gènes aux écosystèmes. A cela s'ajoute l'échelle de temps, et l'échelle spatiale. Cette phrase soulève ainsi un problème conceptuel fondamental en écologie et peut-être à l'origine de la phrase de **Lawton (1999)**: « ecology is a mess ». A l'heure actuelle, les scientifiques analysent la diversité à une plus grande échelle biotique, spatiale, et temporelle pour en déduire les déterminants majeurs et prédire l'impact des changements futurs (Table I.1; **Levin 1992, Petersen *et al.* 2003, Fritz *et al.* 2013, Hatton *et al.* 2015**).

Table I.1 Répartition des chapitres de cette thèse sur les échelles d'étude, spatiale, biotique, et temporelle.

	Echelle Spatiale	Echelle Biotique	Echelle Temporelle
Chapitre 1	Locale	Populations	Durée vie communauté
Chapitre 2	Régionale	Communautés	Instantané
Chapitre 3	Biogéographique	Communautés	Instantané
Chapitre 4	Locale	Individus	Durée vie individus
Chapitre 5	Locale	Communautés	Durée vie communauté
Chapitre 6	Biogéographique	Communautés	Durée vie communauté

3.1 Peut-on extrapoler la réponse des communautés à partir de la réponse des espèces?

L'échelle biotique qui va des gènes aux écosystèmes définit dès le départ de l'étude le patron de diversité. Cette diversité est taxonomique si on se préoccupe de la richesse spécifique, fonctionnelle si on prend en compte le rôle et les traits de ces espèces, et phylogénétique si on étudie leur génome (Figure I.4). Dans un contexte de changements environnementaux, un des problèmes est d'essayer d'extrapoler la réponse de la communauté à partir de la réponse des espèces qui la composent. Cependant, une perturbation sur une communauté est subie directement par chacune des espèces mais peut aussi impacter indirectement les autres espèces via le réseau d'interaction **(Barton & Ives 2014)**. Les conséquences de telles réactions en chaîne sont bien souvent imprédictibles et nécessitent la connaissance de la biologie de chacune des espèces (Chapitre 4; **Rosset & Oertli 2011**). Si l'environnement agit directement sur le phénotype des organismes qu'en est-t-il de son influence sur le génotype sous-jacent et donc le potentiel évolutif de l'espèce? La diversité phylogénétique est un patron que je n'ai pu traiter lors de ma thèse, mais qui, je pense, mériterait l'attention des écologues et généticiens. En ce sens, l'étude de la phylogénie des communautés d'invertébrés aquatiques à différentes échelles spatiales (plante, population de plante, biogéographique) conduirait à de stimulant horizons de recherche sur la représentation de la niche des espèces et du fonctionnement des écosystèmes **(Flynn *et al.* 2011, Srivastava *et al.* 2012)**.

3.2 Les patrons, observés localement, se répètent-ils à des échelles spatiales plus larges?

L'accumulation d'observations à l'échelle locale a permis aux écologues d'étudier explicitement, ces dernières décennies, l'influence des échelles spatiales sur les patrons de diversité **(Chase & Leibold 2002, Petersen *et al.* 2003, Fritz *et al.* 2013)**. Il semble de plus en plus évident que le remplacement des espèces entre localités favorise l'importance de processus locaux diminuant, de fait, l'importance des processus biogéographiques **(Jardine 2014)**. Pour pallier cette dépendance au contexte local certains auteurs proposent d'utiliser les groupes fonctionnels **(Lamanna *et al.* 2014, Violle *et al.* 2014)**, une démarche utilisée avec succès dans les travaux de cette thèse (Chapitres 3 et 6). Par exemple, la lumière, à travers un couvert végétal différentiel, a un effet sur les communautés aquatiques dans tous les sites d'étude mais il n'est pas consistant au travers des échelles spatiales traduisant des effets locaux importants (Chapitre 3). De même, la magnitude et la direction de la réponse aux scénarios de précipitation changent localement (Chapitre 6). Ces deux études nous démontrent en revanche l'importance des filtreurs et des odonates dans le fonctionnement du milieu aquatique quelle que soit la localité, ainsi que l'importance de l'hydrologie dans la sélection des plantes par les organismes terrestres sous contrainte de la présence des interactions biotiques.

3.3 Prise en compte de la dynamique temporelle des communautés?

L'étude temporelle des changements de patrons de diversité est coûteuse en moyens matériels et humains, conduisant dans certains cas à substituer le temps par l'espace. Les deux approches sont, néanmoins, complémentaires. Deux points importants sont à considérer lorsqu'on prend en compte l'aspect dynamique des communautés dans les protocoles expérimentaux **(Petersen *et al.* 2003)**: i) la durée de l'expérience par rapport aux temps de générations et aux temps de réponse des organismes à la perturbation, et ii) la fréquence des perturbations simulées par rapport à l'effort d'échantillonnage et la durée de l'expérience. La majorité des espèces aquatiques des broméliacées à réservoirs complètent la partie aquatique de leur cycle de vie en moins de deux mois (Chapitre 1). Ces résultats confirment et insistent sur une durée minimum de deux mois lors de manipulation expérimentales sur ces écosystèmes miniatures **(Ngai & Srivastava 2006, Trzcinski *et al.* en révision)**.

L'étude de la dynamique temporelle de la communauté d'organismes terrestres (Chapitre 6), ne nous a pas permis de détecter significativement des patrons d'interactions entre les espèces (*e.g.*, évitement ou attraction). L'effort d'échantillonnage (observations journalières) est pourtant en adéquation avec la fréquence et l'intensité des perturbations simulées. De plus, la durée de deux mois de l'expérience couvre largement le temps de réponse (comportement) de ces organismes. Une explication à ce manque de significativité provient de l'utilisation de grands groupes fonctionnels empêchant ainsi de détecter la réponse différentielle des différentes espèces au sein de ces groupes. Ces résultats soulignent la difficulté de modéliser les variations d'occurrences journalières des organismes terrestres en réponse à des modifications des facteurs biotiques (présence d'autres espèces) et abiotiques (précipitations, hydrologie des plantes).

Finalement, les tendances passées et actuelles peuvent nous aider à prédire, avec un certain degré d'incertitude, l'impact des changements futurs **(Diffenbaugh & Giorgi 2012, Fritz *et al.* 2013)**. L'utilisation de microcosmes naturels (broméliacées, trous d'arbres et de roches …) en écologie expérimentale n'est pas nouvelle **(Lawton 1995, Carpenter 1996)**, mais reste marginale. Les résultats des travaux de cette thèse constituent une ligne de base du fonctionnement de l'écosystème broméliacée en conditions naturelles et faiblement anthropisées. Le suivi de ces modèles d'étude pourra éventuellement nous permettre d'observer l'impact des changements environnementaux sur ces communautés **(Richardson *et al.* 2015)**.

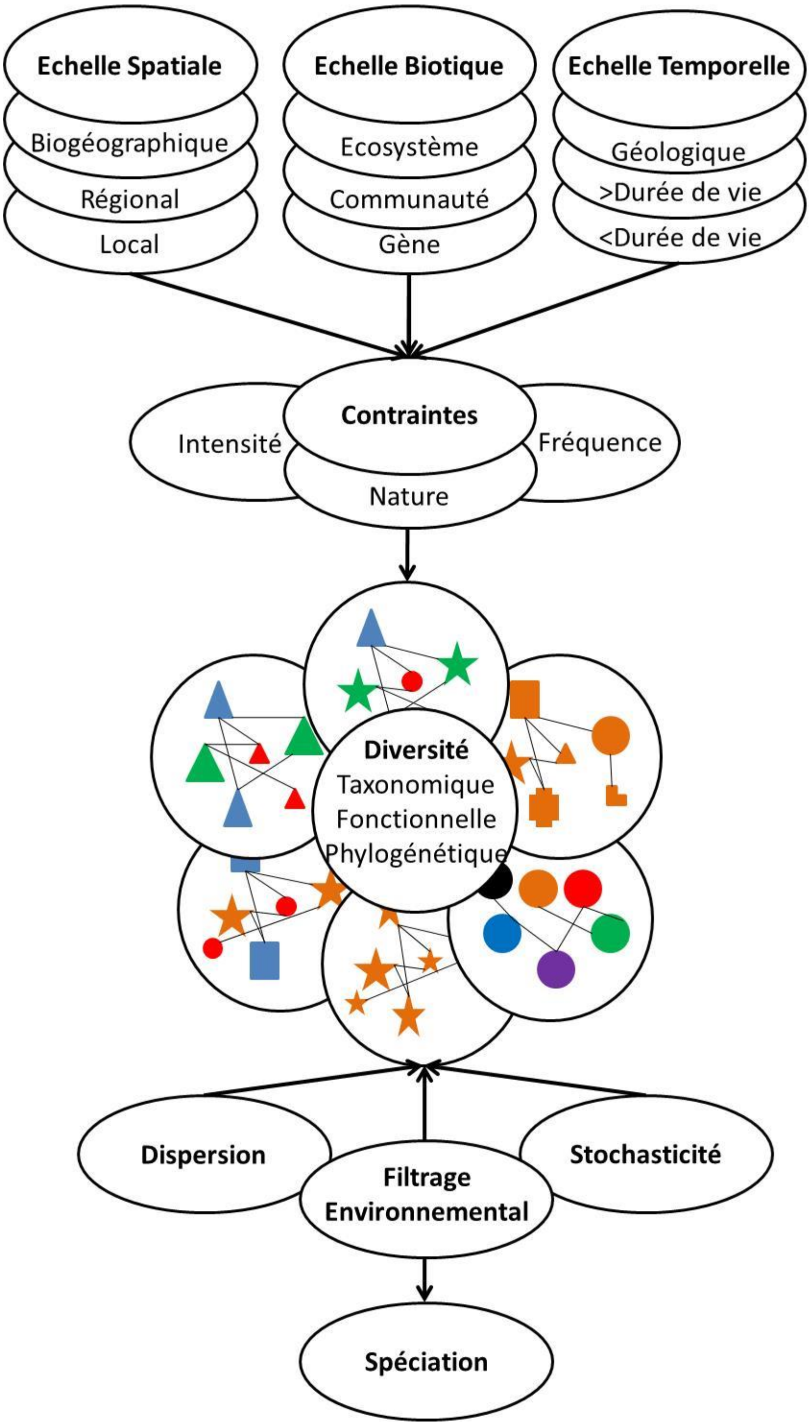

Figure I.4 En écologie, à partir du moment où on définit les échelles d'étude on oriente directement le cadre conceptuel, les tests, et les observations d'un système donné. Ces échelles sont au nombre de trois: spatiale, biotique, et temporelle. Selon l'échelle choisie, les contraintes varient. Par exemple, si on se place à une échelle spatiale locale sur un ou plusieurs individus, les contraintes qui limitent le développement des individus peuvent être les interactions antagonistes ou des perturbations environnementales. Si on se place ensuite à une échelle spatiale plus importante, la contrainte limitante n'est peut-être plus les interactions entre individus mais la capacité de dispersion. Faire varier ces échelles pour étudier différents aspects de la biodiversité (diversité taxonomique, fonctionnelle, et phylogénétique), permet en retour de déterminer les mécanismes dominants de structuration de la diversité: dispersion, filtrage environnemental, et stochasticité. Ultimement, les espèces évoluent via la spéciation.

4 Ecosystèmes miniatures: est-ce que la taille compte?

Peut-on transposer la réponse d'écosystèmes miniatures à celle d'écosystèmes aquatiques plus grands (ou plus petits)? L'intérêt de la réponse à cette question ne réside pas tant dans l'applicabilité des résultats d'écosystèmes plus petits à ceux d'écosystèmes plus grands (ou *vice et versa*), mais plutôt de la précision avec laquelle on arrive à dégager les similitudes et les dissimilitudes.

4.1 Des écosystèmes, en apparence, dissimilaires

De prime abord, la dynamique d'un écosystème de petite taille est particulièrement déterminée par les perturbations externes. Par exemple, l'eau contenue dans les trous d'arbres et les rochers présentent une faible inertie face aux évènements de sécheresse, comparé aux écosystèmes plus grands **(Sota *et al.* 1994, Brendonck *et al.* 2015)**. Ces petites masses d'eau s'assèchent, piègent les organismes, créant ainsi des zones refuges ou sources et des zones sèches ou puits (Chapitre 5). A l'inverse, dans un lac, pour une sécheresse donnée, la hausse de température va modifier le phytoplancton et donc la ressource à la base du réseau, induire une stratification thermique de la colonne d'eau, et perturber ainsi les mouvements de nutriments **(Lake 2011)**. Néanmoins les organismes aquatiques peuvent ajuster leurs comportements à cette stratification thermique par la migration verticale **(Adrian *et al.* 2009)**. Pour un épisode de sécheresse donné, le fonctionnement d'écosystèmes miniatures va donc être ralenti ou s'arrêter localement alors que ceux de plus grandes tailles auront pendant un moment, un fonctionnement différent.

En conséquence, les extinctions locales, les capacités de dispersion des espèces, et l'influence de la structure spatiale et des perturbations sur les communautés semblent plus probables dans la dynamique d'écosystèmes miniatures. **Srivastava et al. (2004)** suggèrent d'exprimer la dispersion et la perturbation par rapport au temps de générations des espèces pour pouvoir comparer l'importance de la dispersion et des perturbations sur des écosystèmes de tailles différentes. La dispersion n'est donc plus la distance qui relie un point A à un point B mais le temps qu'il faut mettre pour les relier par rapport à la durée du cycle de vie de l'espèce considérée. De même, l'intensité et la fréquence des perturbations seraient peut-être similaires entre différents écosystèmes une fois rapportées à la durée du cycle de vie des espèces.

Si cette perspective de recherche semble intéressante, comprendre *a priori* les liens qui unissent les temps de génération à la dispersion, aux processus spatiaux, et aux perturbations, est une nécessité. Premièrement, **Meutter et al. (2007)** démontrent que ces liens ne sont pas évidents. Les contraintes qui déterminent la dispersion ne sont donc pas forcément identiques à celles qui limitent le temps de génération. Deuxièmement, dans les écosystèmes miniatures, les temps de génération des espèces sont courts (< 6 mois). Les écosystèmes plus grands accueillent des espèces dont les cycles de vie durent de quelques jours, à plusieurs mois et années. En ce sens, l'expression de la dispersion ou de la perturbation par rapport au temps de génération serait dépendent du taxon considéré et bien plus variable dans les écosystèmes plus larges. Bien que ces écosystèmes soient, en apparence, différents, nous verrons, dans la suite de cette discussion, que les points communs, entre la structure et les processus sous-jacents, sont nombreux.

4.2 Des ressemblances plus nombreuses que les dissemblances: la structure des réseaux

L'accumulation d'études sur les écosystèmes miniatures indique qu'ils ne sont pas si différents d'autres écosystèmes plus larges (mares, lacs) ou plus petits (bractées d'*Heliconia*). Par exemple, les densités des micro-organismes atteignent des valeurs similaires à celles des mares et des lacs productifs **(Carrias *et al.* 2001)**. De même, l'influence des cascades trophiques, les principaux groupes fonctionnels (filtreurs, brouteurs, collecteurs, prédateurs, déchiqueteurs), et une ressource essentiellement basée sur la décomposition de la matière organique ont été mis en évidence dans les broméliacées (Chapitre 2; **Srivastava & Bell 2009**), les trous d'arbres **(Fincke *et al.* 1997)**, les rivières **(Wallace & Eggert 2009)**, et les lacs **(Rejas *et al.* 2005)**.

Les résultats du Chapitre 1 démontrent que la production secondaire soutenue par les broméliacées à réservoirs est comparable à celle d'écosystèmes plus grands, et soulignent le lien étroit avec la matrice terrestre environnante. Cette relation entre écosystèmes adjacents a déjà été documentée pour des milieux lentiques et lotiques **(Gratton & Vander Zanden 2009)**. Cette forte production secondaire est, en partie, expliquée par la composition taxonomique des communautés aquatiques de broméliacées à réservoirs. On peut alors se demander à quel point la diversité taxonomique d'écosystèmes miniatures recoupe celle d'écosystèmes plus grands? On supposerait alors que la diversité taxonomique de ces microcosmes représente un sous-ensemble de celle des macro-écosystèmes. Une synthèse des caractéristiques physiques des habitats aquatiques a été faite **Downing et al. (2006)** et complétée par **Lehner et al. (2011)** mais aucun de ces auteurs ne prend en compte les écosystèmes miniatures et encore moins la diversité taxonomique. On estime pourtant que 50 millions de broméliacées à réservoirs se développent au Brésil **(Haubrich *et al.* 2009)** ce qui représenterait un sixième de l'abondance des lacs dans le monde **(Downing *et al.* 2006)**.

4.3 Les mécanismes sous-jacents sont identiques: le filtrage environnemental, la dispersion, et la stochasticité

Le filtrage environnemental stipule que les espèces sont sélectionnées localement par des contraintes biotiques et/ou abiotiques selon leurs traits fonctionnels augmentant alors le chevauchement des niches. Ce mécanisme est important dans le système broméliacées car il se retrouve dans tous les travaux de cette thèse à partir du moment où on associe les traits ou adaptations des espèces à leur milieu. Son importance varie néanmoins en fonction des échelles spatiales auxquelles on se place (Figure I.4). Par exemple, à une échelle régionale le filtrage agit sur la composition spécifique des communautés via la lumière (Chapitres 2 et 3), mais à une échelle locale, c'est-à-dire où la lumière est homogène, les espèces différencient leur niches spatialement ou temporellement à cause de l'exclusion compétitive (Chapitre 1). Ce mécanisme est aussi mis en exergue dans le fonctionnement des lacs via l'étude de l'influence de gradients environnementaux **(Declerck *et al.* 2005, Carvalho & Tejerina-Garro 2015)**.

La dispersion des invertébrés est inhérente à un système organisé en métacommunauté et dont 90% de la biomasse est représentée par des espèces ayant des cycles de vie complexes (stades aquatiques et adultes ailées). Notre connaissance du rayon de dispersion est pourtant très limitée pour la plupart des taxons considérés. On effleure ce sujet dans la discussion du Chapitre 5, où on suppose que l'intensification d'une sécheresse à une échelle spatiale régionale aurait un impact drastique sur la résilience du système via la dispersion (Figure I.4). On peut aller plus loin dans la réflexion en étudiant comment la dispersion différentielle des espèces, passive ou active (la phorésie ou le vol d'adultes ailés; **Farjalla *et al.* 2012**) interagit avec la structure du couvert végétal et la connectivité du milieu environnant **(LeCraw *et al.* 2014a)**. Ce fonctionnement en métacommunauté est bien connu sur les mares des climats tempérées **(Cottenie 2005, De Meester *et al.* 2005, Vanschoenwinkel *et al.* 2013)**.

Le hasard, la stochasticité ou la dérive écologique en biologie évolutive, relève de l'imprédictibilité d'un phénomène qui survient indépendamment des traits des espèces et conduit localement toutes les espèces, à l'exception d'une seule, à l'extinction. Je ne referai pas, ici, l'historique du débat entre les partisans d'un tout déterministe ou d'un tout stochastique mais prendrai parti pour une influence des deux. Un constat évident est le biais des études sur le hasard en faveur d'organismes sessiles comme les plantes. Qu'en est-il du hasard dans le règne animal? On peut observer son influence au travers de perturbations biotiques comme la suppression d'une part du patrimoine génétique des espèces aquatiques indépendamment de leur adaptation aux conditions environnementales à cause du singe qui va manger une plante, de l'arbre qui tombe sur lequel il y a une population de broméliacées à réservoirs ou du chercheur qui va échantillonner une population et les stocker dans du formaldéhyde. En ce sens, trois principales sources de stochasticité influencent les communautés écologiques: l'échantillonnage, les extinctions locales, et la dispersion aléatoire **(Vellend 2010)**.

Le hasard est-il uniquement inhibiteur de diversité? Certains auteurs voient le hasard dans le comportement des espèces, notamment les gazelles en fuite devant un guépard font preuve d'imprédictibilité **(Pavé 2011)**. Cette flexibilité comportementale augmente alors les chances de survie lorsque le prédateur court plus vite que la proie. Un des prédateurs dominant à l'apex du réseau trophique des broméliacées à réservoirs en Guyane Française est *Toxorhynchites*. Par contre, au Costa Rica, le prédateur principal présent dans les broméliacées est l'odonate alors que *Toxorhynchites* est occasionnellement détecté. Ce dernier se retrouve en abondance dans les trous d'arbres de cette région. Ces observations peuvent être perçues comme du bruit ou une valeur aberrante en statistique mais ne serait-ce pas là une manifestation du hasard? Une mutation des gènes codants pour l'organe sensoriel à la base de la sélection d'habitat va pousser l'insecte à aller pondre dans une broméliacée au lieu du trou d'arbre, est-ce une erreur, de l'opportunisme, ou le hasard? Le filtrage ou la sélection va ensuite déterminer sa persistance dans le milieu. En ce sens, une impressionnante majorité des articles se concentrent sur les espèces ayant un poids important dans les processus écosystémiques. Nous ne dérogeons pas à ce constat lorsqu'on s'est concentré sur les 11 espèces qui représentaient 90% de la biomasse du système (Chapitre 1). Qu'est ce qui détermine la présence des 11 espèces rares restantes ? Le hasard, au travers de la variabilité intraspécifique, ne pourrait-il pas partiellement expliquer la présence de ces espèces touristes ou rares? Nos résultats ne peuvent mettre en évidence l'influence du hasard sur les communautés mais la littérature récente offre de belles perspectives quant à sa détection, notamment dans des mares artificielles **(Chase 2007, Chase 2010)** et autres systèmes (voir la synthèse de **Vellend *et al.* 2014**). L'utilisation d'écosystèmes miniatures semble tout indiquée pour discriminer l'importance relative des différents processus d'assemblage des communautés.

4.4 Quelle que soit la taille de l'écosystème, les espèces évoluent

De façon ultime, le potentiel évolutif des espèces est impacté à hauteur de la rapidité des changements environnementaux. Si les prédictions de l'**IPCC (2013)** convergent vers une augmentation de 1 à 4°C d'ici 2100, cela veut dire qu'en l'espace de 85 ans et avec 5 générations par an, *Cyphon* sp., le coléoptère dominant en Guyane Française aura le temps de voir passer 425 générations, les ostracodes 510 générations (85*6 générations), et les Culicidae 2040 générations (85*24 générations, Chapitre 1). Si les changements les plus rapides affectent les espèces ayant les temps de génération les plus longs et la fécondité la plus basse alors *Cyphon* sp. est relativement le plus en danger. Si cet impact est en plus influencé par les capacités de dispersion des espèces alors les ostracodes qui dispersent via phorésie, sont plus en danger. Cependant ces derniers sont capables de produire des formes de résistance et de se reproduire par parthénogénèse faisant de ce taxon un candidat robuste aux changements environnementaux. Ces traits d'histoire de vie exacerbent la difficulté de relier la dispersion, le temps de génération, et les changements environnementaux. Parce que les temps évolutifs peuvent interférer avec les temps écologiques **(Hairston *et al.* 2005, Massol 2008)**, il devient urgent d'essayer de quantifier la réponse génétique des espèces sous contraintes de perturbations environnementales et d'associer les traits fonctionnels qui ont la plus grande influence sur la valeur sélective des espèces **(De Meester *et al.* 2011)**.

5 Perspectives de recherche et conclusion

En regard des résultats obtenus lors de cette thèse, des données acquises ces dernières années sur les broméliacées à réservoirs, et du contexte actuel de l'écologie, trois pistes de recherches principales semblent se dégager à court et à long termes.

5.1 Flux de matière aux écotones aquatiques-terrestres: influence des changements environnementaux sur le couplage d'écosystèmes adjacents

La stabilité des réseaux trophiques des broméliacées à réservoirs est assurée par un cœur d'espèces généralistes (Chapitre 2), et peut être influencée par l'hétérogénéité naturelle des habitats **(Dézerald *et al.* 2014)** ou par des perturbations d'origine anthropique (Chapitre 5). De plus, une large fraction de la biomasse hétérotrophe produite par les broméliacées est exportée vers le milieu terrestre via l'émergence d'adultes (Chapitre 1) au bénéfice de taxons terrestres. En plus des araignées prédatrices d'invertébrés émergents, des fourmis peuvent être associées aux broméliacées et augmenter la quantité de ressources à la base du réseau aquatique (Chapitre 4; **Leroy *et al.* 2013, Talaga *et al.* 2015**). Les interactions entre organismes terrestres et aquatiques peuvent être perturbées via une augmentation de la température (Chapitre 4) ou des variations des régimes de précipitations (Chapitre 6). Ensemble, ces résultats suggèrent que la stabilité du réseau trophique aquatique et terrestre dépend étroitement du degré de couplage entre les deux écosystèmes adjacents.

Si l'importance des flux réciproques entre écosystèmes adjacents a été documentée en milieux tempérées **(Polis *et al.* 1997, Nakano & Murakami 2001, Fausch *et al.* 2002, Baxter *et al.* 2005)**, la prévalence de ces mouvements de matière en milieux tropicaux hautement diversifiés est, à ma connaissance, moins étudiée. L'identification des effets d'une perturbation qui soit commune à deux milieux contrastés apporterait une vision plus intégrative du fonctionnement des écosystèmes dans un contexte de changements environnementaux. En ce sens, cette proposition pourrait se décliner en deux objectifs. Le premier objectif tenterait d'analyser comment des perturbations d'origine anthropique peuvent affecter les flux d'organismes et de matière entre écosystèmes adjacents. Le deuxième proposerait de déterminer si la stabilité de ces flux dépend des caractéristiques physiques de l'écosystème considéré.

Si le signe et la magnitude de la réponse des flux étaient dépendants des caractéristiques de la perturbation, on peut supposer que le degré de couplage entre réseaux trophiques aquatiques et terrestres pourrait exacerber (couplage faible) ou temporiser (couplage fort) les effets de cette perturbation. Le test de cette hypothèse consisterait à manipuler expérimentalement les quantités/abondances de matière, d'invertébrés émergents et/ou de prédateurs terrestres et aquatiques, sous différents scénarios de perturbations. Finalement, le deuxième objectif pourrait être accompli en effectuant une méta-analyse de la productivité relative d'écosystèmes contrastés (*e.g.*, taille, surface de contact avec le milieu terrestre, complexité) à la manière de **Gratton et Vander Zanden (2009)** mais en incluant les écosystèmes miniatures. Ces auteurs concluent, qu'à l'échelle du paysage, la contribution relative d'écosystèmes lotiques et lentiques à la production secondaire totale dépend de leurs nombres et de leurs tailles. En dépit de leurs petites tailles, les broméliacées supportent une production secondaire qui est comparable à celle d'écosystèmes plus grands (Chapitre 1). On peut alors supposer que l'ajout de ces écosystèmes miniatures dans les modèles de **Gratton et Vander Zanden (2009)**, conduirait à prendre en compte seulement le nombre.

5.2 Distribution de la diversité taxonomique et des traits fonctionnels des réseaux trophiques le long d'un gradient de temporalité des écosystèmes aquatiques

Le fonctionnement d'un écosystème est la résultante de l'interaction entre les changements environnementaux, qu'ils soient d'origine naturelle et/ou anthropique, et les espèces responsables de la capture, de la conversion, et des flux d'énergie et de matière (Chapitre 5). Bien plus que la diversité taxonomique, les traits fonctionnels déterminent comment les espèces affectent et répondent à leur environnement, représentant alors de meilleurs indicateurs de la niche occupée par la communauté **(McGill *et al.* 2006, Violle *et al.* 2007)**. De plus, le fort renouvellement de la composition spécifique entre écosystèmes ou zones géographiques, limite la portée des résultats de comparaisons entre écosystèmes/échelles d'étude **(Violle *et al.* 2014)**. Comprendre comment les diversités taxonomiques et fonctionnelles sont distribuées, présente de larges implications théoriques sur les processus de structuration et de maintien de la biodiversité et des implications plus appliquées à la conservation de milieux contrastés.

Cette perspective propose ainsi d'évaluer le degré de spécificité taxonomique et fonctionnelle des communautés d'invertébrés le long d'un gradient de temporalité des écosystèmes aquatiques. Ce gradient de temporalité serait, dans ce cas, approximé par les caractéristiques physiques de ces écosystèmes (*e.g.,* tailles, limites, ratios du volume par la surface de contact avec le milieu terrestre). Si l'intensité du filtrage environnemental (taille, vulnérabilité du système à la sécheresse) est inversement corrélé à la diversité spécifique (Chapitre 1) et positivement corrélé à la convergence des traits fonctionnels (Chapitre 5), on peut supposer que i) deux espèces, tirées aléatoirement des communautés de broméliacées, seraient fonctionnellement plus similaires que deux espèces tirées au hasard des communautés des mares, rivières ou lacs, ii) les structures taxonomiques et fonctionnelles des communautés de milieux temporaires seraient des sous-ensembles de celles de milieux plus stables (écosystèmes plus larges), et iii) ces sous-ensembles seraient principalement constitués d'un « cœur » d'espèces généralistes/ubiquistes.

Pour tester ces prédictions, il serait intéressant d'effectuer une méta-analyse prenant en compte les plus petits écosystèmes (Chapitre 1; **Brendonck *et al.* 2015**), étangs/mares **(Boersma *et al.* 2014)**, rivières en tresses **(Gray & Harding 2007)**, rivières **(Lake 2003)**, et les lacs **(Adrian *et al.* 2009, Céréghino *et al.* 2012)** à l'extrémité opposée du gradient. Cependant, un constat évident à la lecture de cette littérature est le biais des études en faveur de milieux aquatiques des climats tempérés (*e.g.,* Europe, Amérique du Nord, et en moindre mesure, en Australie). La plupart des données de diversité d'invertébrés aquatiques en milieux tropicaux proviennent d'études sur la qualité des eaux dont les objectifs sont de déterminer des indices biotiques de perturbation des milieux (voir la thèse de **Dedieu 2014** sur l'influence de l'orpaillage sur les petites criques en Guyane Française). Une analyse très préliminaire sur des données non publiées en Guyane Française (données non publiées de **Dedieu 2014**) démontre que 59% des familles des broméliacées à réservoirs sont communes aux petites masses d'eau (PME), et aux masses d'eau de transition (MET). A l'inverse, ce pourcentage de similarité entre les trois milieux tombe à 14% et 24% pour les PME et MET. Ces chiffres ne tiennent pas compte des efforts différentiels d'échantillonnage entre ces milieux (variabilité spatio-temporelle), mais promettent de stimulantes perspectives de recherche.

5.3 Structure phylogénétique des réseaux trophiques le long d'un gradient de temporalité des milieux

Les distances phylogénétiques représentent indirectement une mesure du temps écoulé depuis la divergence et l'évolution indépendante entre deux espèces **(Batalha *et al.* 2015)**. Actuellement, peu d'études ont exploré comment la structure phylogénétique des communautés influençait le fonctionnement des écosystèmes **(Rezende *et al.* 2007, Bersier & Kehrli 2008, Gomez *et al.* 2010)**, en dépit des possibilités offertes par cette approche **(Mouquet *et al.* 2012)**. En effet, la diversité phylogénétique (avec la diversité fonctionnelle) semblerait avoir un plus grand pouvoir prédictif et explicatif des interactions entre espèces comparé à la diversité taxonomique **(Flynn *et al.* 2011)**. Cependant, la plupart des études ont examiné les communautés végétales ou microbiennes, réduisant le panel d'interactions à un seul niveau trophique plutôt qu'entre différents niveaux **(Srivastava *et al.* 2012)**.

Toujours dans un contexte de changements environnementaux, cette troisième perspective propose d'utiliser nos connaissances de la diversité fonctionnelle, et d'étudier la structure phylogénétique des réseaux trophiques pour répondre à deux principales questions. Comment est distribuée la diversité phylogénétique le long d'un gradient de temporalité des écosystèmes? Comment la diversité phylogénétique interagit avec la diversité fonctionnelle le long de ce même gradient? Pour répondre à ces questions, il faudrait construire les arbres phylogénétiques des organismes aquatiques de tous les milieux aquatiques d'une zone donnée (broméliacées à réservoirs, trous d'arbres, flaques, mares, criques, *etc.*), et déterminer où ils se situent sur cet arbre en fonction de leurs différents milieux de vie. Si le filtrage environnemental (E) induit une convergence des traits fonctionnels (T) des communautés le long d'un gradient de temporalité des milieux, E→T, alors deux hypothèses alternatives sont possibles: i) le signal phylogénétique (P) est fortement conservé à la suite de ce filtrage, E→T→P, et/ou ii) l'environnement et la structure phylogénétique influencent indépendamment les traits fonctionnels, E→T←P.

Finalement, je suppose depuis le début que l'environnement induit une convergence des traits fonctionnels mais la coexistence stable de plusieurs espèces est possible uniquement si leurs traits ou similarités phylogénétiques divergent pour minimiser le chevauchement des niches. Si ces prédictions sont, en apparence, contradictoires, je suppose que ce dernier problème ne serait que le reflet de la variabilité des échelles d'étude utilisées. En effet, la convergence des traits serait observée si on se place sur un large gradient environnemental, c'est-à-dire entre plusieurs milieux différents, à l'inverse la divergence serait visible si on se place au sein d'un milieu homogène.

En conclusion, les flux d'énergie sont le propre de la nature car chaque individu a besoin de se nourrir pour vivre et se reproduire. Les interactions trophiques sont, je pense, les liens majeurs qui relient les individus au fonctionnement des écosystèmes. Les contraintes auxquelles ces écosystèmes sont exposés varient selon les échelles d'étude considérées **(Jacob 1977)**, le but étant de déterminer les ressemblances et les dissemblances lorsqu'on passe d'un niveau de complexité à l'autre **(Levin 1992)**. Les échelles biotiques, spatiales, et temporelles représentent alors les filtres de l'objectif photographique qui prend en photo la roue écologique, en ce sens, les écologues ne réinventent pas la roue, ils la prennent en photos avec des filtres différents.

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GLOSSAIRE

Biodiversité mesure de la richesse d'entités biologiques dans une communauté; on la qualifie de diversité taxonomique si on évalue le nombre d'espèces, de fonctionnelle si on mesure les traits des espèces, et de phylogénétique si on détermine les génotypes dans une population).

Changements environnementaux ensemble des modifications des conditions environnementales biotiques et abiotiques, d'origine naturelle ou anthropique

Communauté écologique ensemble d'espèces partageant des ressources communes

Contraintes facteurs biotiques et abiotiques limitant la présence, la survie, la croissance, et le succès reproducteur des individus, populations, et espèces dans l'espace et dans le temps.

Ecosystème vision holistique d'une communauté avec une attention particulière portée sur l'aspect fonctionnel

Métacommunauté ensemble de communautés connectées par la migration/dispersion des espèces

Réseau trophique ensemble d'espèces liées par des flux d'énergie, les consommateurs et les ressources, par exemples les prédateurs consomment des proies, et les organismes autotrophes utilisent la lumière, l'eau et les minéraux.

Stabilité capacité de la dynamique d'un système à résister à une contrainte, à retourner à l'état initial suivant l'arrêt de cette contrainte, et à fluctuer périodiquement et de façon persistante dans le temps