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# The closer the better? Relative influence of forest continuity and distance to water on the taxonomic and functional structure of riparian plant communities along headwater streams

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Running head: high value of ancient forests near stream

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**ABSTRACT**

**Questions:** (1) Is forest temporal continuity an important factor in structuring the riparian plant communities along small alluvial valleys? (2) To what extent can distance from the stream modulate the effect of forest continuity and provide a better understanding of the taxonomic and functional structure of these communities?

**Location:** Ouanne watershed, France.

**Methods:** We used a paired samples design, involving stands close and far from the stream, in ancient or recent riparian forests, in which we studied the vegetation. We performed analyses of species richness and cover, as well as mean values of species preferences and functional traits, and measures of species composition, distinguishing between the understory and overstory.

**Results:** Strong differences in richness and mean values, as well as in composition, were found between ancient and recent forests. Ancient forests were characterized by species with a dominant stress-tolerant strategy, whereas recent forests were dominated by hygrophilous and nitrophilous species with a dominant competitive strategy. Furthermore, we found that ancient and recent stands close to the stream encompassed a larger richness of species, than ancient and recent riparian stands far from the stream, a pattern mostly driven by the greater co-occurrence of small ruderal species with rapid leaves turnover but also of ancient forest species.

**Conclusions:** In small riparian forest stands along headwater streams, we have shown that past human activities leave still detectable traces in contemporary plant communities. In addition, we pointed out that colonization by ancient indicator species was faster in recent forests closer to the stream. This underscores the need to protect remaining ancient riparian forests that are well connected to the stream, even if they are small, and suggests that bank reforestation as well as restoration of hydrological connectivity on rivers fragmented by artificial barriers may be an effective way to increase forest biodiversity in riparian zones.

Keywords: ancient forests, connectivity, conservation, creek, distance to stream, forest continuity, functional traits, legacy effect, riparian vegetation.

## INTRODUCTION

Historical ecology has demonstrated the legacy effects that past land uses can have on the properties of contemporary forest ecosystems and associated biodiversity (Peterken & Game 1984; Hermy et al. 1999; De Frenne et al. 2011). Changes in land cover over time can often be deduced from historical land-use maps, such as the Ordnance Survey Map in Great Britain, the Val der Maelen Map in Belgium or the État-Major Map in France. With these maps, it is possible to determine precisely whether a site has been occupied by forest at different times and thus to characterize the so-called 'forest continuity', also referred as 'forest ancientness' or 'ancient woodland' (Flinn & Vellend 2005; Goldberg et al. 2007; Hermy & Verheyen 2007). More precisely, this characterization makes it possible to distinguish between ancient forests, which have been forested continuously for centuries, and recent forests, i.e. newly established forests resulting from spontaneous afforestation on former agricultural land or artificial plantations (also known as 'second growth' or 'post-agricultural forests'). Forest continuity thus refers to the maintenance of forest cover over time, irrespective of stand maturity and management type. It influences forest biodiversity through two mechanisms, a dispersal limitation, related to increased exposure time to colonization, and a recruitment limitation, related to changes in soil properties and competitive interactions (Flinn & Vellend 2005; Hermy & Verheyen 2007).

Research that has linked biodiversity to the temporal continuity of forest cover has mainly studied the response of vascular herbaceous plants in lowland temperate forests, particularly in northwestern Europe (De Frenne et al. 2011). Numerous studies have shown that the composition of plant species differed between ancient and recent forests and several regional lists of ancient forest plant species have been developed (e.g. Hermy et al. 1999; Matuszkiewicz et al. 2013; Bergès et al. 2016). The response of other taxa - insects (e.g. Assmann 1999), lichens (e.g. Janssen et al. 2019), fungi (e.g. Spake et al. 2016) – to forest continuity has also been studied, and despite variations in the magnitude and significance of the effects, have overall highlighted the importance of ancient forests for conservation. However, although some studies have been carried out in areas other than temperate lowland forests, as is the case in mountain and Mediterranean areas (Sciama et al. 2009; Janssen et al. 2018; Abadie et al. 2018), several forest types have been largely ignored in historical ecology (Bergès & Dupouey 2021). This is especially the case for riparian forests, i.e., forests at the interface between freshwater and terrestrial ecosystems, usually established on riverbanks.

Riparian forests, although representing only 1% of the European continental surface (Weissteiner et al. 2016), host a unique species pool and are of critical concern for biodiversity conservation (González et al. 2017). This

strong ecological interest is, however, threatened by numerous anthropogenic pressures affecting riparian vegetation either directly, e.g. by clearing vegetation, or indirectly, e.g. by altering the flow regime through dams (González et al. 2017). Although the extent of riparian forests has increased sharply since the 1950s in western Europe, due to the natural afforestation of stabilized floodplains and to large plantations of hybrid poplars (Liébault & Piégay 2002; Archaux & Martin 2009), a large part of the natural riparian vegetation has already been lost, degraded or fragmented. There is thus an urgent need to preserve existing intact riparian vegetation and better assess the conservation value of the remaining ancient riparian forests. This is particularly true in headwater streams, where the harvesting of forest stands bordering creeks may threaten the quality of downstream ecosystems (Richardson & Danehy 2007; Suurkuukka et al. 2014).

Here, we combined a taxonomic and functional approach, to test whether forest continuity influences the structure of plant communities in small remnant riparian forest stands along creeks. This double approach allows both a focus on conservation issues, studying variations in species richness and identity, and a better understanding of the underlying ecological processes captured by functional traits (i.e. Westoby's Leaf-Height-Seed), species preferences for habitat conditions (i.e. Ellenberg's indicator values) and ecological strategies deployed along disturbance and stress gradients (i.e. Grime's CSR). Based upon a dedicated sampling design in which we selected ancient and recent riparian forest stands, either in close proximity to stream or far from the bank, we more precisely tested whether the distance to the water changed the taxonomic and functional response of plant communities to forest continuity. This has been motivated by the fact that the dispersion of plant along streams is to a large part dependent on floods (Nilsson et al. 2010; Bourgeois et al. 2016), which should not only favour the arrival of a higher density of propagules but also a better recruitment of species (Glaeser & Wulf 2009). However, although a few studies have shown differences in the species composition of ancient and recent forests in large alluvial valleys (Verheyen et al. 2003; Glaeser & Wulf 2009; Douda 2010; Chevalier et al. 2014), no studies have yet focused on forest fragments bordering creeks in headwater systems and none have tested the interaction between forest continuity and distance from the stream. In order to fill this knowledge gap, we addressed the following two questions: (1) Is temporal continuity of forest cover an important factor in the taxonomic and functional structuring of riparian plant communities in forest stands along headwater streams? (2) To what extent can distance from the stream modulate the effect of forest continuity and provide a better understanding of the taxonomic and functional structure of riparian plant communities?

## MATERIALS & METHODS

### Study area and experimental design

The study was carried out along the headwater area of the Ouanne creek (size of study area watershed = 950 km², stream width = 2-6 m, mean annual discharge at Toucy gauging station = 0.976 $m^3/s$) and its tributaries in the center of France (Figure 1). These small alluvial valleys are under the influence of punctual and irregular floods that cause disturbances of small spatial extent, i.e. often limited to riparian stands directly in contact with the stream. They are characterized by a temperate climate with oceanic influences (mean annual temperatures of 11.6°C and annual precipitations ranging between 700 and 800 mm) and a geological context dominated by acidic silts and flint clays. To limit variation in environmental conditions, the study area was restricted to the alluvial part of streams, made up of modern alluvial deposits and colonized by forests dominated by European alder (*Alnus glutinosa*), field maple (*Acer campestre*), European hornbeam (*Carpinus betulus*) and European ash (*Fraxinus excelsior*). The surrounding landscape is mainly composed of agricultural areas, consisting of vast fields of crops and pastures, and wooded areas more or less connected to each other. During the summers of 2018 and 2019, we sampled 24 sites in ancient (n = 12) or recent (n = 12) riparian forests. For each site, we studied the vegetation in a pair of stands (n stands = 48), one directly in contact with the stream, referred to as “close to stream” (ancient = 12, recent = 12), the other remote from the stream, referred to as “far from stream” (ancient = 12, recent = 12) (Figure 1). Each pair was established on the same stream segment and positioned in small adjacent riparian forest fragments, averaging 1.46 ha in size. The distinction between stand close and far from the stream was made by establishing a buffer zone of 5 to 10 m between the boundaries of the two stands where vegetation was surveyed (Figure 1). Forest continuity was characterized by crossing digitized and geo-referenced 1:40,000 État-Major maps of France, charted in 1837 for our study area, with 1:10,000 up-to-date forest maps (BD Forêt® V2) in a Geographic Information System (QGIS Development Team 2015). Forest cover overlapping in both maps was considered to indicate ancient forests (i.e. with a continuity of forest cover well above 180 years), while current forest cover overlapping with crops or meadows in the État-Major maps was considered to indicate recent forests (i.e. with a continuity of forest cover well below 180 years). To confirm the continuity of the forest cover since the middle of the 19$^{th}$ century, we used a series of aerial photographs taken in 1950 at and around each site. Combined with an inspection of the most recent aerial photographs available, this approach allowed us to prospect for polygons occupied by

134 forests with a natural appearance, i.e. avoiding poplar groves or harvested plots. Finally, to avoid biases due to
135 low accuracy of vegetation mapping from historical land use maps, isolated polygons < 0.25 ha and < 20 m wide
136 were eliminated.

137 **Vegetation survey**

138 At the scale of the stand (i.e. ancient-close, ancient-far, recent-close, recent-far), vegetation surveys were
139 realized following the Braun–Blanquet abundance-dominance methodology. Within a 200-m² (20 m x 10 m)
140 rectangular plot, parallel to the stream, a complete inventory was done in June/July, either in 2018 (n = 26) or
141 in 2019 (n = 22). All the vascular plants (pteridophytes and phanerogams) were recorded by considering two
142 layers, that of the overstory (i.e. tree and shrub layers ≥ 2 m height) and that of the understory (i.e. herbaceous
143 layer < 2 m height). To limit biases associated with observer effect, all surveys were performed by the same
144 experienced botanist (RC), assisted by colleagues, considering an average search effort of 30 min per plot.

145 **Stand and soil data**

146 At the scale of the site (ancient forests, n pairs = 12; recent forests, n pairs = 12), stand and soil data were
147 measured only in the stand far from the stream. This was motivated by the fact that the overstory composition
148 and structure of these riparian forests were homogeneous between stands close and far from the stream.
149 Stand attributes were characterized using a series of nested circular subplots: a 4-m-radius subplot to measure
150 trees with a diameter at breast height (DBH, at 1.3 m standard height) ≥ 5 cm, a 6-m-radius subplot for DBH ≥
151 10 cm, a 9-m-radius subplot for DBH ≥ 25 cm and a 15-m-radius subplot for DBH ≥ 45 cm. For each tree,
152 species, diameter and vitality state (alive, dying, dead), were recorded. Soil properties were characterized using
153 a soil corer in the stand center to describe the soil texture classes at 20-cm depth, based on the Jamagne's
154 (1967) texture triangle, and estimated the percentage of coarse elements (Ø > 2 mm) in the first 50 cm of soil.
155 Humus forms, i.e. mull, moder, mor and their subdivisions, were described based on three sampling points
156 located 2 m from the plot center in opposite directions. Finally, the coordinates of the stand center and the
157 elevation difference with the stream water level were measured using a GPS device and an inclinometer
158 respectively.
159 From the field measurements, we calculated a set of variables to compare environmental conditions between
160 ancient and recent forests. Stand variables (basal area of living trees and of dead trees, number of 5-cm
161 diameter classes, canopy cover percentage), were standardized to a per hectare basis and used to compare
162 overstory characteristics. Soil variables (percentage of sand/silt/clay and of coarse elements) were derived

either from direct measurements or from the conversion of texture classes to percentage using the central value of the texture triangle. Humus forms were converted to a quantitative assessment using the humus index proposed by Ponge et al. (2002). These soil variables were used to highlight possible legacy effects of past human activities on edaphic conditions or pre-existing differences in environmental conditions. Spatial (latitude and longitude) and topographic (altitude and elevation from water) variables were used to control for possible biases in the distribution of sites within the study area.

**Plant preference and trait data**

To analyze how the ecological preferences and strategies of plants differed according to forest continuity and distance from the stream, we collected data for each species from three sources of information. Ellenberg's indicator values (Ellenberg et al. 1992) for light (L), nutrient availability (N) and soil moisture (F) were extracted from the Baseflor database (Julve 1998) and used to characterize variations in species habitat preference. Among the 194 species encountered, these values were unavailable for three species with a single occurrence in our data set (i.e. singleton species) and for five taxa identified at the genus level. Grime's values (Grime 1977) for respectively Competitors, Stress-tolerators and Ruderals, i.e. ternary coordinates, were extracted from the list of species available in Pierce et al. (2017) and used to characterize variations in the strategy–environment relationships of riparian plants. For missing values (n = 54), data were either completed by using ecological information on closely related species, i.e. mean value for the same genus (n = 43), or discarded (genus level taxa, n = 4; singleton species, n = 2; others, n = 2). Westoby's values for specific leaf area (SLA; leaf area per dry mass), plant height at maturity and seed mass were extracted from the LEDA database (Kleyer et al. 2008) and used to characterize variations in resource acquisition, competitive and dispersal abilities. Missing values were restricted to ten taxa (genus level taxa, n = 4; singleton species, n = 4; others, n = 2).

At the scale of each forest stand (n = 48), we then computed the mean values weighted by the relative cover of each species bearing each value, i.e. community-weighted means (CWMs) (FD package, Laliberté et al. 2014). Since herbaceous species are the most sensitive to forest continuity (Gilliam 2007) and tree species can be shaped by forestry practices, CWMs were calculated only for herbaceous understory species.

Finally, to analyze how ancient forest species differed according to forest continuity and distance from the stream, we used three local species lists of plants (Hermy et al. 1999; Dupouey et al. 2002; Bergès et al. 2016) and considered as ancient forest indicator a species that appears at least twice in these lists.

**Statistical analysis**

To determine whether environmental parameters varied between ancient and recent forests (n = 24), we used the Mann-Whitney U-test. For proportional data (i.e. sand, silt, clay, soil coarse elements and canopy cover), logit transformation was applied prior to the calculation.

To determine whether species richness and cover, as well as the mean values of species' preferences and traits, were influenced by forest continuity, distance to stream and their interaction, we used linear mixed models (LMMs) in which "Sites" (n = 24) was included as a random effect (lme4 package, Bates et al. 2015). This random effect is designed to control for the non-independence of observations made in paired stands close to or far from the stream. For taxonomic measures, we used the total richness and cover of forest overstory and understory species as well as the richness and cover of ancient forest indicator species as dependent variables (Appendix S1). For mean values, we used as dependent variables CWMs related to species preferences (light, nutrient availability and soil moisture), ecological strategies (competitors, stress-tolerators and ruderals) and functional strategies of plants (SLA, height and seed mass) (Appendix S1).

To determine whether species composition was influenced by forest continuity, distance to the stream and their interaction, we used multivariate generalized linear models (GLMs) (mvabund package, Wang et al. 2012). We fitted the full model, testing the interaction between forest continuity and distance of the stream to each species that was present in more than 5% of the stands, using presence-absence data, with a binomial distribution and summed the likelihood ratio statistics across the univariate responses to estimate their multivariate response. Because overstory composition can influence the recruitment of ancient-forest species (Thomaes et al. 2014) and because tree composition can change within a few decades during riparian succession (Schnitzler 1995; Fierke & Kauffman 2005; Janssen et al. 2020), we fitted one multivariate GLM for the understory and one for the overstory. The significance of the factors 'forest continuity' and 'distance to stream' in the multivariate GLM was assessed using an analysis of variance with the PIT-trap method and 999 bootstrap resamples (Warton et al. 2017). This method has the advantage of using a resampling scheme that ensures that p-values are approximately correct when the independence assumption is not satisfied, as is the case of our paired sampling design. To determine which herbaceous and tree species best contribute to the overall model deviation, we extracted univariate test statistics and adjusted p-values for each species, using the Holm's step-down procedure to correct for multiple testing (for details see, Wang et al. 2012). Finally, to provide a graphical representation of the two main factors and their interaction, we used a canonical analysis

of principal coordinates (CAP, Anderson & Willis 2003) with the Jaccard distance community matrix (vegan package, Oksanen et al. 2013).

Analyses were performed with R version 4.0.0 (R Core Team 2020).

## RESULTS

### Variations in environmental conditions between ancient and recent riparian forests

Mann–Whitney U-test revealed that only the humus index varied significantly with forest continuity, being more acidic in ancient forests than in recent forests. All others environmental variables did not vary with forest continuity (Appendix S2), indicating that ecological conditions were comparable between ancient and recent forests in the studied area.

### Effect of forest continuity and distance to stream on species richness and cover and mean indicator and traits values

A total of 194 vascular plant species have been inventoried on the 48 forest stands, of which 34 species have been identified as ancient forest indicator species. At stand scale, overstory richness ranged from 4 to 13 species (mean ± SD = 8 ± 2.31), understory richness ranged from 14 to 58 species (mean ± SD = 36 ± 11.9), while ancient plant richness ranged from 3 to 18 species (mean ± SD = 8 ± 3.77).

LMMs revealed no significant interaction between forest continuity and distance to stream (Table 1). The richness and cover of ancient forest species and the mean Grime value for stress-tolerators were significantly higher in ancient forest stands, while the richness and cover of overstory vegetation, the mean Ellenberg value for soil moisture and nutrient availability, as well as the mean Grime value for competitors were significantly higher in recent forest stands. Also, the richness of understory vegetation, the richness and cover of ancient forest species, the mean Ellenberg value for nutrient availability, the mean Grime value for ruderals and the mean value for SLA were significantly higher close to the stream, while the mean Grime value for stress-tolerators and the mean value for plant height were significantly higher far to the stream.

### Effect of forest continuity and distance to stream on the species composition of overstory and understory

The multivariate GLM for understory vegetation showed that species composition varied significantly with forest continuity (Deviance = 259.8, p = 0.001) and distance to the stream (Deviance = 179.5, p = 0.007), but not with their interaction term (Deviance = 75.9, p = 0.617). Based on the deviation explained by factors, most of the variation in species composition was related to differences between ancient and recent forests, as

shown by the first CAP-axis (Figure 2-A). The second axis was more evidently related to the distance to the stream. Univariate tests for each species showed that few of them contributed significantly to the multivariate significant effect (Table 2). Among the species that captured the largest amount of the deviance explained by forest continuity, *Angelica sylvestris* and *Filipendula ulmaria* were more frequent in recent forests, while *Milium effusum* and *Carex sylvatica* were more frequent in ancient forests. For the distance to the stream, species that captured the largest amount of the deviance, i.e. *Veronica montana*, *Stellaria holostea*, *Elymus caninus* and *Phalaris arundinacea*, were all more frequent in stands close to the stream (Appendix S3).

The multivariate GLMs for overstory vegetation showed that species composition varied significantly with forest continuity (Deviance = 99.3, p = 0.001) but neither with distance to the stream (Deviance = 19.9, p = 0.643), nor with the interaction term (Deviance = 15.6, p = 0.719). The strong forest continuity effect is well represented by the first CAP-axis (Figure 2-B), which shows clear difference in species composition between ancient and recent forests. Univariate tests for each species showed that few of them contributed to the multivariate significant effect. Among the trees/shrubs that captured the largest amount of the deviance explained by forest continuity, *Alnus glutinosa*, *Sambucus nigra* and *Corylus avellana* were more frequent in recent forests, while *Carpinus betulus* was more frequent in ancient forests (Appendix S4).

## DISCUSSION

In accordance with the large amount of previous studies in European temperate forests (Hermy et al. 1999; De Frenne et al. 2011; Matuszkiewicz et al. 2013; Bergès et al. 2016), we found that past land uses leave still detectable traces in contemporary riparian plant communities. This highlights that even in narrow strips of riparian forests along small streams, and in addition to the numerous environmental factors that structure riparian communities, it is important to consider forest continuity to better understand biodiversity patterns (Verheyen et al. 2003; Glaeser & Wulf 2009; Douda 2010). In addition, we showed that plant species richness, including that of ancient forest indicator species, was higher in stands near the stream, and that this effect was found both in ancient and recent forests. This suggests that the restoration of the hydrological connectivity on rivers fragmented by artificial barriers (e.g. weirs and bed sills) could be an effective way to increase forest biodiversity (Glaeser & Wulf 2009). Overall, by showing that ancient riparian forest stands, even if small in size, supported distinct assemblages of plant species, our results highlight their strong ecological interest and the need to better conserve the remaining fragments in agricultural landscapes.

**Forest continuity strongly influences riparian communities of headwater streams**

Our results showed that the richness and cover of overstory vegetation was higher in recent riparian forest stands than in ancient ones. This may be related to the maintenance of shrubs in early successional stages (Douda 2010), as confirmed by univariate analyses for each species (Appendix S4), when forest gradually colonized former agricultural lands (Bergès & Dupouey 2021). This may also be related to a higher level of available resources in recent forests (Hermy et al. 1999; Herault & Honnay 2005; Sciama et al. 2009), which should favor a higher density of individuals and benefit a larger diversity of species (i.e. species-energy hypothesis, Wright 1983). Indeed, Ellenberg's values support the view that nutrient availability was greater in recent than in ancient forests, due to legacy effects of past agricultural practices or pre-existing differences in soil properties, thus conditioning past land uses. Our results also showed that the richness and cover of ancient forest species were significantly higher in ancient forests (Hermy & Verheyen 2007). This confirms the validity of previously established lists (Hermy et al. 1999; Dupouey et al. 2002; Bergès et al. 2016), even in the riparian context (Douda 2010; Chevalier et al. 2014), and, as ancient forest species represent a guild of specialists sensitive to habitat loss and fragmentation (Bergès & Dupouey 2021), it pleads for priority conservation of ancient forest stands, even of small size, along the banks of headwater streams. Specifically, our results showed that the Grime's ecological strategies were different between ancient and recent forests, dominated by stress-tolerators in the first case and by competitors in the second. Those results are consistent with previous ones (Hermy et al. 1999; Hermy & Verheyen 2007; Douda 2010) and reflect a filtering of plants species in relation to available environmental conditions, less limited by resources and leading to greater competitive interactions between vigorous species in recent forests. However, due to overall more fertile habitat conditions, it has been shown that the recruitment of ancient forest species was faster in recent forests in alluvial valleys than in non-alluvial contexts (Dumortier et al. 2002; Verheyen et al. 2003). Our results tend to confirm this, since of the 34 ancient forest species recorded in our study area, 26 were inventoried in recent forests. This indicates that habitat conditions in recent riparian forests are globally favorable to the recruitment of ancient forest species and suggests that restoration actions promoting the reforestation of riverbanks could benefit forest biodiversity (McClain et al. 2011) as well as that of streams (Suurkuukka et al. 2014). Regarding species composition, we found significant differences between ancient and recent forest stands. For the understory, these results are consistent with those reported in temperate forests (De Frenne et al. 2011; Matuszkiewicz et al. 2013; Bergès et al. 2016), including riparian forests (Verheyen et al. 2003; Glaeser & Wulf

307 2009; Douda 2010). As such, among the herbaceous species that predominantly occurred in ancient forests,
308 numerous were already listed as ancient forest indicator species, e.g. *Milium effusum*, *Carex sylvatica* or *Vinca*
309 *minor* (Hermy et al. 1999; Dupouey et al. 2002; Bergès et al. 2016). Interestingly, our results also emphasized
310 plants indicative of recent forests, which are usually found in wetlands (Douda 2010), e.g. *Angelica sylvestris*,
311 *Caltha palustris* or *Filipendula ulmaria*. Beyond showing that understory composition responds consistently to
312 increasing soil moisture in recent forests, as expressed by Ellenberg values, our results highlight that recent
313 forest species captured most of the explained deviance. This suggests recent forest species have a higher
314 indicative power than ancient forest species and thus, that relevant lists of recent forest plants (Bergès et al.
315 2016) may be a complementary tool for identifying the continuity of forest cover in areas lacking historical
316 land-use maps or where their accuracy is too coarse. Our results also highlighted differences in the composition
317 of overstory. This can be attributed to different maturation stages between ancient forests, dominated by the
318 post-pioneer species *Carpinus betulus*, and recent forests, dominated by the pioneer species *Alnus glutinosa*.
319 Associated with changes in humus forms, these results reveal the difficulty of disentangling the effects of forest
320 continuity from those of forest succession. Indeed, it has been shown that changes in canopy composition
321 (Thomaes et al. 2014) and maturity stage (Janssen et al. 2018) of stands can induce a shift in herbaceous
322 communities in ancient forests. Thus, although the difference in successional stage may partially explain the
323 understory changes between ancient and recent forests, the fact that all other environmental variables did not
324 vary with forest continuity supports the idea of a strong effect left by past human activities in the studied
325 alluvial valleys.

326 **Stream proximity enhances the conservation value of riparian forests**

327 Total understory and ancient forest species richness was higher in stands located near the water. On the one
328 hand, and linked to the predictions of the species-energy hypothesis (Wright 1983), this difference can be
329 attributed to more fertile habitat conditions, as expressed by the increase in the mean Ellenberg value for
330 nutrient availability near the stream. Indeed, in our predominantly agricultural study area, it is possible that
331 nutrient leaching into streams preferentially enriches the best-connected adjacent riparian zones. On the other
332 hand, this effect can be attributed to more frequent and intense floods in the stands closest to the stream. This
333 assumption is supported by the fact that not only the richness of ruderals but also the mean value of specific
334 leaf area increased in stands close to the stream, while the mean value of plant height decreased. Given that
335 ruderal species are fast-growing with an annual life cycle (Grime 1977), that high SLA values indicate the

dominance of “acquisitive” species with rapid leaf turnover, and that smaller species indicate a shorter potential growth duration between disturbances (Westoby 1998), our results provide strong evidence that near-stream herbaceous communities are adapted to a more disturbed environment. Another important point is related to the potential of colonization, which is known to increase along flooded areas due to the addition of hydrochorous species to the local species pool (Jansson et al. 2005; Nilsson et al. 2010). However, contrary to expectations, the mean value of seed mass did not increase with distance to the stream. Although seed traits have been demonstrated to explain long-distance dispersal patterns (Nilsson et al. 2010; Bourgeois et al. 2016), local patterns of seed deposition may be less dependent on seed morphology, especially along creeks. Indeed, in headwater streams, it has been shown that non-hydrochores can successfully disperse by water flow (Honnay et al. 2001) but also that propagules can be caught and carried away by floating debris (Nilsson et al. 2010). We therefore infer that the positive effect of stream proximity on richness patterns was mainly due to flooding which increased both disturbances and colonization opportunities in ancient and recent forest stands. Specifically, the fact that almost all of the recent forests studied were a short distance downstream from ancient forests may explain why they received more ancient forest species than stands far from the stream (Honnay et al. 2001).

Regarding species composition, significant differences were found for understory vegetation but not for overstory vegetation between stands close and far from the stream. These results thus confirm that riparian forest stands belonged to the same successional stage in each pair of stands but also that distance to water strongly structures herbaceous communities. Indeed, on riverbanks, the distance to the stream is most often related to an elevation gradient and, by extension, to the flood gradient, well known for its great importance in the structuring of riparian communities (Naiman & Decamps 1997; Poff et al. 1997). As such, numerous studies have documented strong shift in species and traits composition from the bottom to the top of the riverbank (Kyle & Leishman 2009; McCoy-Sulentic et al. 2017). Thus, although no differences in Ellenberg values for soil moisture were found between stands close and far from the stream, in the riparian forests studied, we infer that compositional changes were related to spatial variations in flood frequency and intensity as well as in nutrient availability. In stands close to the stream, flooding, by periodically disturbing understory vegetation but also by providing nutrients, may have favored the establishment of species requiring fertile environments (e.g. *Alliaria petiolata*, *Elymus caninus*, *Phalaris arundinacea*) and/or ruderals (e.g. *Stellaria holostea*, *Veronica montana*, *Viola reichenbachiana*).

## CONCLUSION

Using a dedicated sampling design, we demonstrated that stand position relative to the stream and forest continuity strongly shaped riparian plant communities, even for small wooded patches in headwater streams. Specifically, we show that in fertile and humid riparian forests, the colonization credit usually documented in non-alluvial settings appears to resolve more rapidly, at least for the recent forests closest to the stream. These results complement well the few previous studies carried out in large alluvial valleys (Verheyen et al. 2003; Herault & Honnay 2005; Glaeser & Wulf 2009; Douda 2010) and give weight to the need to increase the conservation of the remaining ancient riparian forests. Moreover, by showing that recent forests established along streams were rapidly colonized by ancient forest species, our results suggest that riverbank reforestation actions could be an effective way to increase the forest biodiversity. In Europe's predominantly agricultural landscapes, this knowledge provides complementary arguments to encourage the conservation and restoration of ancient forests. This is particularly the case along headwater streams, which account for up to 80% of the total length of streams in watersheds around the world (Gomi et al. 2002).

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## AUTHOR CONTRIBUTIONS

R.C. conceived the research idea and collected data; P.J. performed statistical analyses; P.J., wrote the first draft of the paper; all authors discussed the results and commented on the manuscript.

## DATA ACCESSIBILITY

The research data supporting this publication are provided in the online supporting information.

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**SUPPORTING INFORMATION**

Appendix S1: Correlation matrix of dependent variables

Appendix S2: Variations of environmental variables in relation to forest continuity

Appendix S3: Univariate tests for understory species

Appendix S4: Univariate tests for overstory species

Appendix S5: Raw data: environmental variables

Appendix S6: Raw data: species by sites matrix

**Table 1.** Mean (±SD) of species richness and species cover, as well as of the community-weighted means of trait value, in relation to forest continuity (ancient vs recent) and distance to stream (close vs far) along the Ouanne creek and its tributaries, France (p-value based on linear mixed models).

| | Variable | Ancient forests | | Recent forests | | Forest | Distance | Interaction |
|---|---|---|---|---|---|---|---|---|
| | | close | far | close | far | continuity | to stream | |
| | | Mean (±SD) | Mean (±SD) | Mean (±SD) | Mean (±SD) | p value | p value | p value |
| Richness and cover | Overstory richness | 6.83 (±1.70) | 6.33 (±1.92) | 9.42 (±1.31) | 8.50 (±2.78) | 0.001 | 0.197 | 0.700 |
| | Overstory cover | 86.79 (±20.59) | 76.62 (±19.99) | 91.48 (±17.07) | 97.62 (±20.03) | 0.027 | 0.721 | 0.154 |
| | Understory richness | 39.25 (±10.66) | 28.42 (±10.03) | 43.67 (±7.76) | 34.92 (±13.87) | 0.161 | <0.001 | 0.654 |
| | Understory cover | 118.05 (±33.02) | 109.66 (±35.68) | 141.57 (±28.00) | 126.32 (±35.38) | 0.087 | 0.134 | 0.656 |
| | Ancient forest richness | 11.25 (±3.52) | 8.42 (±4.12) | 8.58 (±2.87) | 5.42 (±2.11) | 0.026 | <0.001 | 0.778 |
| | Ancient forest cover | 42.38 (±21.53) | 28.02 (±15.23) | 28.02 (±22.21) | 15.38 (±11.57) | 0.037 | 0.004 | 0.842 |
| Mean value (CWM) | Soil moisture | 5.35 (±0.35) | 5.19 (±0.17) | 5.74 (±0.53) | 5.81 (±0.46) | 0.002 | 0.557 | 0.157 |
| | Light | 4.61 (±0.40) | 4.66 (±0.38) | 4.84 (±0.32) | 4.95 (±0.38) | 0.066 | 0.242 | 0.662 |
| | Nutrient availability | 5.25 (±0.82) | 4.76 (±1.23) | 6.37 (±0.71) | 5.82 (±0.99) | 0.003 | 0.021 | 0.897 |
| | Competitors | 29.12 (±5.89) | 26.95 (±5.45) | 35.94 (±6.42) | 35.81 (±5.06) | 0.001 | 0.369 | 0.426 |
| | Stress-tolerators | 27.70 (±8.83) | 36.67 (±16.17) | 16.61 (±5.98) | 22.68 (±10.86) | 0.003 | 0.007 | 0.569 |
| | Ruderals | 43.18 (±9.19) | 36.38 (±14.35) | 47.45 (±6.96) | 41.52 (±11.32) | 0.246 | 0.004 | 0.829 |
| | Specific leaf area | 27.82 (±5.80) | 23.86 (±6.13) | 31.99 (±4.03) | 27.77 (±6.32) | 0.067 | <0.001 | 0.892 |
| | Plant height | 0.70 (±0.23) | 0.94 (±0.36) | 0.54 (±0.17) | 0.77 (±0.30) | 0.094 | 0.001 | 0.953 |
| | Seed mass | 2.87 (±1.25) | 4.10 (±2.49) | 2.82 (±1.47) | 2.77 (±0.94) | 0.163 | 0.221 | 0.188 |

549 **Table 2.** Top-ranking species (n = 10) among 92 herbaceous species that explained most of the variation in species composition between ancient/recent forests and stands

550 far/close to the stream (Test = univariate test statistics from the multivariate GLM; p = p-values adjusted). To facilitate interpretation, species frequency in either

551 ancient/recent forests or far/close stands is provided (* = ancient forest indicator species).

| Taxa | Forest continuity | | Ancient | Recent |
|---|---|---|---|---|
| | Test | p | | |
| *Angelica sylvestris* | 14.736 | 0.015 | 4.2% | 29.2% |
| *Filipendula ulmaria* | 13.023 | 0.023 | 8.3% | 33.3% |
| *Milium effusum** | 10.759 | 0.104 | 20.8% | 2.1% |
| *Carex sylvatica** | 9.200 | 0.153 | 22.9% | 4.2% |
| *Caltha palustris* | 9.178 | 0.195 | 0.0% | 12.5% |
| *Carex elongata* | 9.178 | 0.219 | 0.0% | 12.5% |
| *Vinca minor** | 9.178 | 0.228 | 12.5% | 0.0% |
| *Glechoma hederacea* | 8.268 | 0.294 | 25.0% | 43.8% |
| *Scrophularia auriculata* | 5.965 | 0.596 | 2.1% | 14.6% |
| *Urtica dioica* | 5.842 | 0.768 | 22.9% | 39.6% |

| Taxa | Distance to stream | | Far | Close |
|---|---|---|---|---|
| | Test | p | | |
| *Veronica montana** | 13.801 | 0.019 | 10.4% | 35.4% |
| *Stellaria holostea** | 12.566 | 0.045 | 2.1% | 22.9% |
| *Elymus caninus** | 11.740 | 0.053 | 12.5% | 35.4% |
| *Phalaris arundinacea* | 9.305 | 0.209 | 0.0% | 12.5% |
| *Veronica chamaedrys* | 9.161 | 0.245 | 2.1% | 18.8% |
| *Atriplex prostrata* | 7.544 | 0.480 | 0.0% | 10.4% |
| *Viola reichenbachiana** | 7.057 | 0.531 | 14.6% | 33.3% |
| *Geum urbanum* | 6.579 | 0.572 | 31.3% | 45.8% |
| *Alliaria petiolata* | 6.261 | 0.684 | 18.8% | 35.4% |
| *Myosoton aquaticum* | 6.019 | 0.741 | 0.0% | 8.3% |

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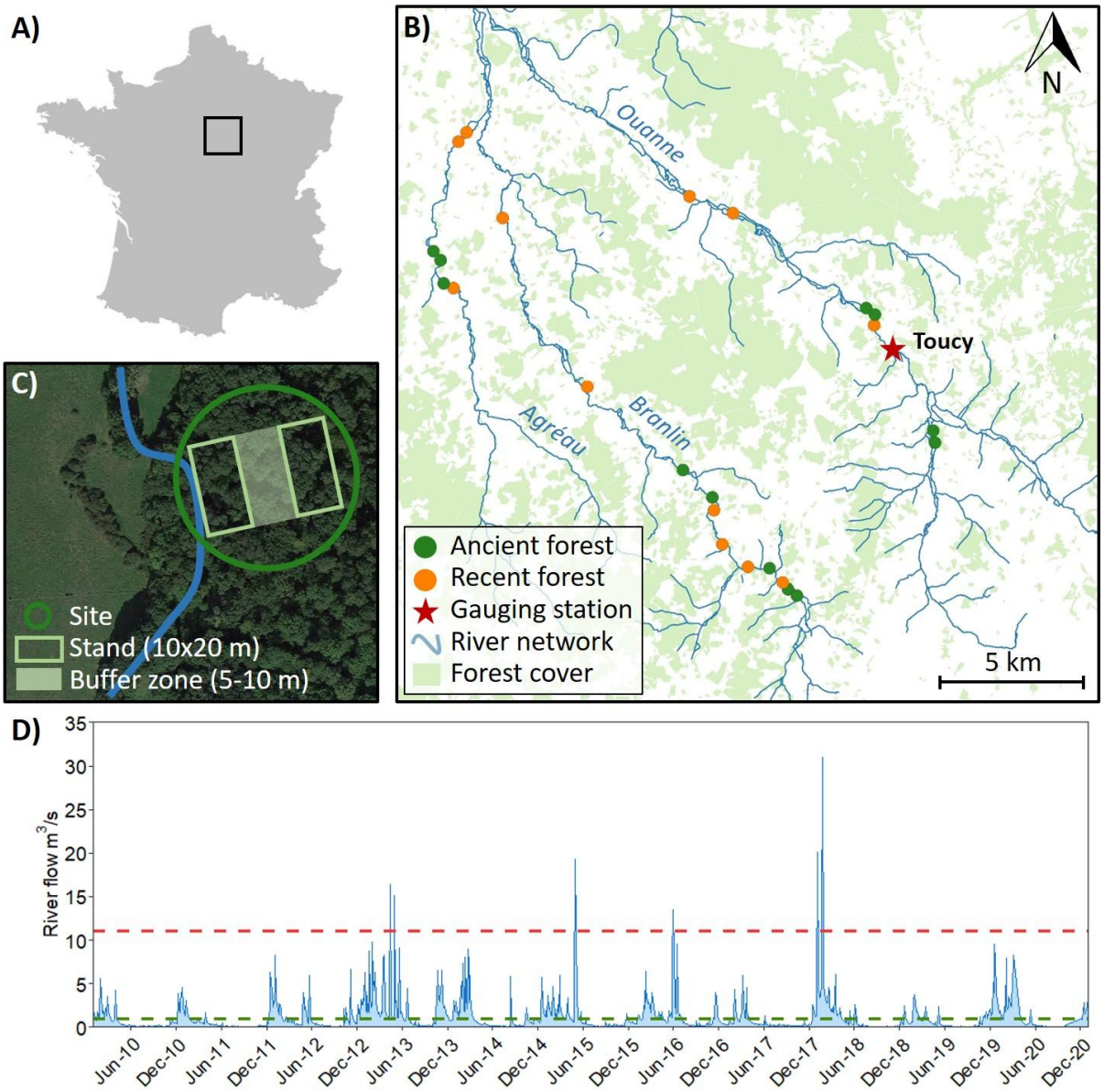
**Figure 1.** Location of the study area in France (A), distribution of sampled riparian forests along the Ouanne creek and its tributaries (B), form of the sampling design used to survey plant communities in relation to their distance to the stream (C) and flow regime variations over the last 10 years at the Toucy gauging station (D,




dashed green line = interannual mean flow; dashed red line = 2-year return flood).

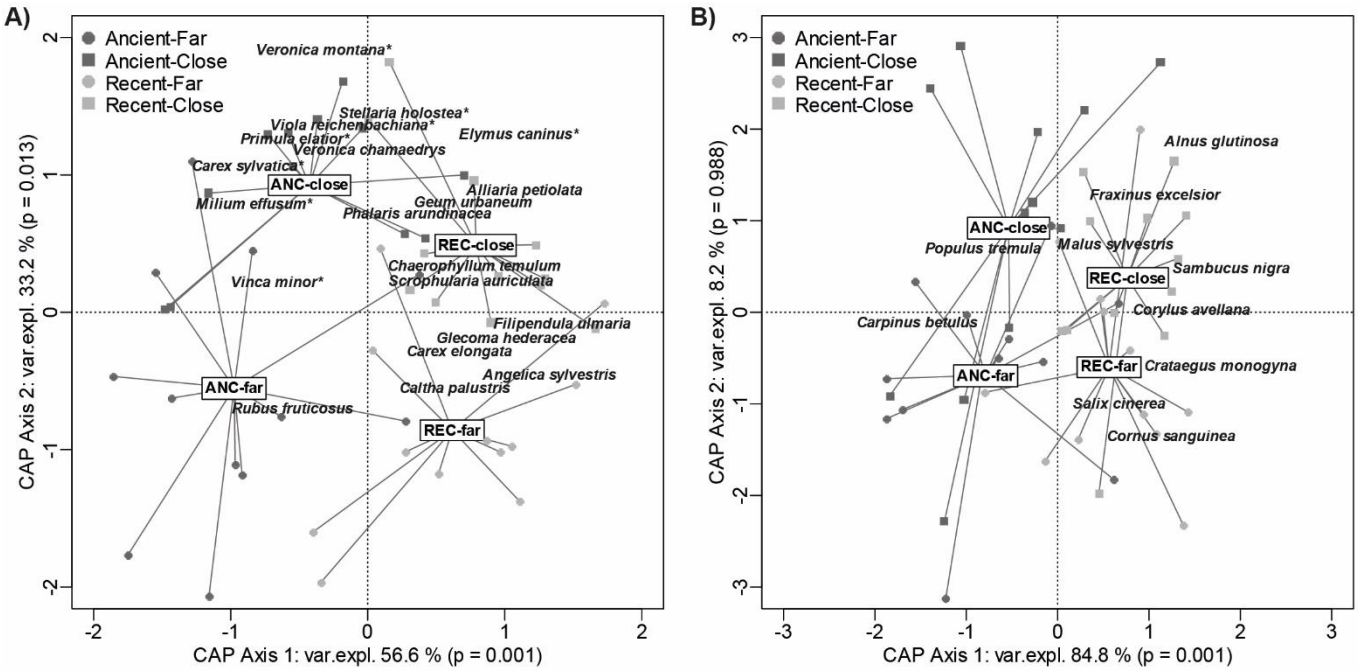



**Figure 2.** Constrained canonical analysis of principal coordinates of riparian understory (A) and overstory (B) communities, for each studied sites along the Ouanne creek and its tributaries, France. To facilitate graphical interpretation, the centroids for the interaction between forest continuity and distance to the stream are provided. In addition, the centroids in principle coordinate space of the most influential (i.e. with the highest cumulative deviance) understory and overstory species are provided (* = ancient forest indicator species, see also Appendix S3 and S4).