

# High ecosystem service delivery potential of small woodlands in agricultural landscapes

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## Abstract

1. Global forest loss and fragmentation have strongly increased the frequency of forest patches smaller than a few hectares. Little is known about the biodiversity and ecosystem service supply potential of such small woodlands in comparison to larger forests. As it is widely recognized that high biodiversity levels increase ecosystem functionality and the delivery of multiple ecosystem services, small, isolated woodlands are expected to have a lower potential for ecosystem service delivery than large forests hosting more species.
2. We collected data on the diversity of six taxonomic groups covering invertebrates, plants and fungi, and on the supply potential of five ecosystem services and one disservice within 224 woodlands distributed across temperate Europe. We related their ability to simultaneously provide multiple ecosystem services (multiservice delivery potential) at different performance levels to biodiversity of all studied taxonomic groups (multidiversity), forest patch size and age, as well as habitat availability and connectivity within the landscape, while accounting for macroclimate, soil properties and forest structure.
3. Unexpectedly, despite their lower multidiversity, smaller woodlands had the potential to deliver multiple services at higher performance levels per area than

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larger woodlands of similar age, probably due to positive edge effects on the supply potential of several ecosystem services.

4. Biodiversity only affected multiservice delivery potential at a low performance level as well as some individual ecosystem services. The importance of other drivers of ecosystem service supply potential by small woodlands in agricultural landscapes also depended on the level of performance and varied with the individual ecosystem service considered.
5. *Synthesis and applications.* Large, ancient woodlands host high levels of biodiversity and can therefore deliver a number of ecosystem services. In contrast, smaller woodlands in agricultural landscapes, especially ancient woodlands, have a higher potential to deliver multiple ecosystem services on a per area basis. Despite their important contribution to agricultural landscape multifunctionality, small woodlands are not currently considered by public policies. There is thus an urgent need for targeted policy instruments to ensure their adequate management and future conservation in order to either achieve multiservice delivery at high levels or to maximize the delivery of specific ecosystem services.

#### KEYWORDS

agricultural landscapes, Anthropocene, biodiversity, ecosystem services, habitat fragmentation, island biogeography, multifunctionality, woodlands

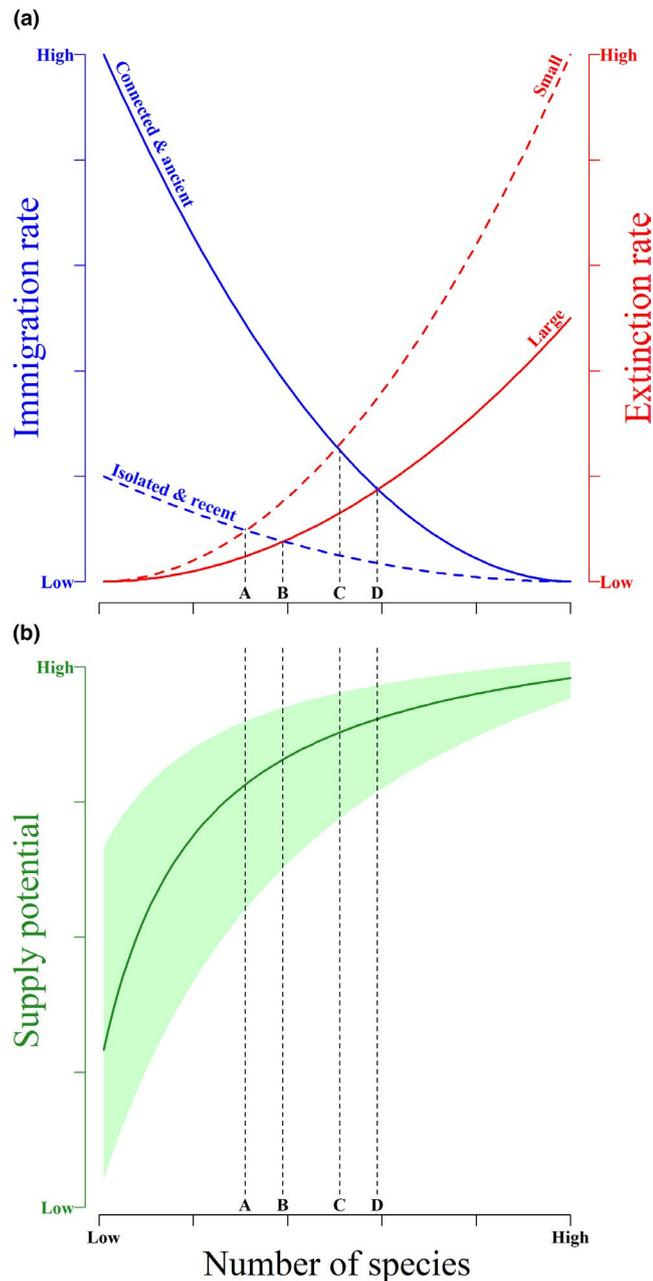
## 1 | INTRODUCTION

Forests deliver a wide range of ecosystem services to human society, and positive relationships between biodiversity and these services have been reported for large forested areas (Gamfeldt et al., 2013; van der Plas et al., 2016). However, there is a lack of knowledge about the relationship between biodiversity and multiple ecosystem services in small woodland patches (Decocq et al., 2016; Mitchell, Bennett, & Gonzalez, 2014). Indeed, in many parts of the world, the original forest cover has been heavily fragmented (Haddad et al., 2015; Hansen et al., 2013) due to human activities; more than 70% of the remaining global forest cover lies within 1 km of a forest edge (Haddad et al., 2015). Many of the remaining woodlands are smaller than 10 ha (Estreguil, Caudullo, de Rigo, & San Miguel, 2013) and scattered in a human-transformed matrix of mostly arable lands, pastures and human settlements. Loss of area, increased isolation and greater exposure to human disturbances along forest edges are leading causes of biodiversity loss (Haddad et al., 2015), although small patch size can sometimes be beneficial for biodiversity, as shown by the preponderance of positive significant responses to habitat fragmentation (Fahrig, 2017).

Small woodland patches in agricultural landscapes also vary in age, since many of them have developed on farmland that was abandoned at different points in time (Flinn & Vellend, 2005). Consequently, small woodlands not only differ in size and degree of

isolation, but also in age, quantified as the time since forest establishment, ranging from very ancient (several centuries or older) to more recent (less than a century). Despite their small size and isolation, patches of (semi-)natural habitats such as small and ancient woodlands can have an important role as refugia for biodiversity (Decocq et al., 2016) and as providers of multiple ecosystem services (Decocq et al., 2016; Mitchell et al., 2014). Therefore, small and ancient forest patches, analogously to other “small natural features” (Hunter, 2017) such as scattered and old trees in agricultural landscapes (Herrera & García, 2009; Manning, Gibbons, & Lindenmayer, 2006; Manning, Fischer, & Lindenmayer, 2009), have an important conservation value. This suggests that the age of these elements in the landscape might also contribute to their conservation value. As it is unknown if the relationships among biodiversity and ecosystem services that emerged from research in large forests (Gamfeldt et al., 2013; van der Plas et al., 2016) apply to small and ancient woodlands, the conservation and management of such elements in agricultural landscapes would strongly benefit from a specific assessment of the drivers of biodiversity and ecosystem service delivery in small woodlands.

The delivery potential of multiple ecosystem services by small and ancient woodlands can be studied by linking the theory of island biogeography (MacArthur & Wilson, 1967) to ecosystem functioning (Figure 1). Large and spatially well-connected forest patches are expected to host more species compared to small



and isolated woodlands (MacArthur & Wilson, 1967). Likewise, patches that have been forested for a long time will likely be more species-rich than recently established forests, which can remain floristically impoverished for centuries (De Frenne et al., 2011) because of the slow immigration rate of forest specialists (Naaf & Kolk, 2015). Together with this variation in taxonomic diversity (Valdés et al., 2015), the functional diversity of patches is expected to vary as well since traits of species colonizing and persisting in, for instance, small, young or isolated patches will differ from those inhabiting large, ancient or well-connected patches (Craven, Filotas, Angers, & Messier, 2016; Vanneste et al., 2019). These functional responses to patch characteristics can in turn affect their functioning and potential for ecosystem service delivery (cf. Suding et al., 2008). Indeed, the effect of taxonomic

**FIGURE 1** Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem functioning for studying the supply potential of multiple ecosystem services by small forest patches. Hypothetical framework on the effects of forest continuity across space and over time on immigration and extinction rates, and thus on the level of biodiversity (i.e. total number of species per forest patch) and the associated supply potential of multiple ecosystem services. (a) MacArthur & Wilson's theory of island biogeography adapted to forest spatiotemporal characteristics (effect of patch connectivity and age on immigration rate and of patch size on extinction rate). (b) Theoretically expected relationship between species richness and supply potential of multiple ecosystem services. The letters along the x-axis (A, B, C and D) depict different landscapes with different expectations on species richness and thus on supply potential of multiple ecosystem services, consisting of: (A) small, isolated and recent forest patches (a lower species richness is expected); (B) large but isolated and recent forest patches (intermediate levels of species richness are expected); (C) small but connected and ancient forest patches (intermediate levels of species richness are expected); and (D) large, connected and ancient forest patches (a higher species richness is expected). The green line and the green shaded polygon depict the average expected relationship between species richness and supply potential of multiple ecosystem services as well as the hypothetical confidence interval of all possible shapes we can expect for this relationship, respectively

or functional diversity on ecosystem functioning and service delivery is widely acknowledged and very well documented in the scientific literature (Balvanera et al., 2006, 2013; Bastian, 2013; Duffy, Godwin, & Cardinale, 2017; Gamfeldt et al., 2013; Lefcheck et al., 2015; van der Plas et al., 2016). In a rigorous quantitative review covering 446 measures of biodiversity effects on ecosystem functioning and services, Balvanera et al. (2006) found clear evidence that biodiversity has positive effects on most of the ecosystem services assessed in their quantitative review. Similarly, a more recent quantitative review focusing on 67 field studies has demonstrated that biomass production, a key ecosystem service, increases with species richness in a wide range of wild taxa and ecosystems (Duffy et al., 2017). This positive relationship between biodiversity and the delivery of single ecosystem services has even been extended to the delivery of multiple services (Gamfeldt et al., 2013; Lefcheck et al., 2015; van der Plas et al., 2016). For instance, higher levels of multiple ecosystem services are found in large forests with more tree species (Gamfeldt et al., 2013). If the positive relationship between biodiversity and the delivery of multiple ecosystem services reported for large forested areas (Gamfeldt et al., 2013; van der Plas et al., 2016) would be fully applicable to small woodlands, we could hypothesize that small, isolated and recent woodlands (cf. situation "A" in Figure 1) would have a lower ecosystem service supply potential (Bodin, Tengö, Norman, Lundberg, & Elmqvist, 2006; Decocq et al., 2016), because they harbor less biodiversity compared to large, connected and ancient forest patches (cf. situation "D" in Figure 1).

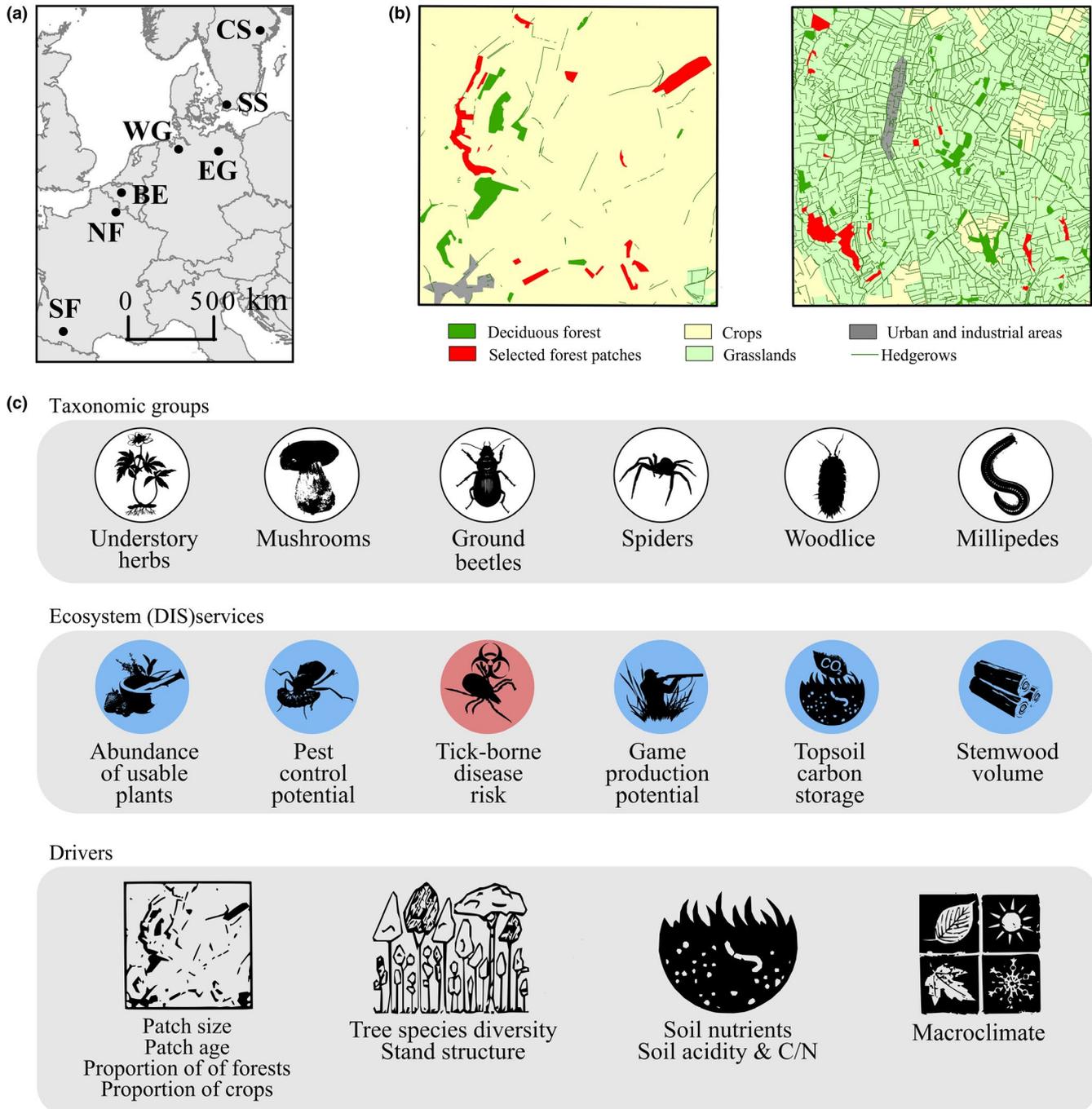
Here, we assessed the supply potential of multiple ecosystem services provided by small (both recent and ancient) woodlands as well as

larger (both recent and ancient) forest patches ( $n = 224$ ) in agricultural landscapes distributed along a 2,500-km latitudinal gradient spanning the entire temperate forest biome in Europe (Figure 2). We collected biodiversity data for six taxonomic groups with different functional roles and dispersal potential, as well as data on the supply potential of six important ecosystem (dis)services delivered by woodlands, representing a mixture of provisioning, regulating and cultural services.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and sampling design

We studied deciduous forest patches in seven regions along a transect spanning c. 2,500 km across the entire temperate forest biome of Europe (Figure 2). In each region, two  $5 \times 5$  km<sup>2</sup> landscape windows



**FIGURE 2** Sampling biodiversity and ecosystem service supply potential in small forest patches in agricultural landscapes. (a) Sampling locations along the 2,500-km latitudinal gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West Germany, EG = East Germany, SS = South Sweden, CS = Central Sweden). (b) Detail of two of the 14 studied landscapes (low vs. high connectivity) in North France, showing the distribution of land uses and the selected forest patches in red. Each landscape is  $5 \times 5$  km<sup>2</sup>. (c) Detail of the six taxonomic groups, six ecosystem services (blue) or disservices (red) and four groups of drivers assessed within each of the selected forest patches

(14 in total) with two contrasting connectivity levels were selected: (a) a 'high-disturbance landscape' with isolated forest patches surrounded by an intensively cultivated matrix, dominated by large open fields with intensive use of pesticides and fertilizers; and (b) a 'low-disturbance landscape' with forest patches more or less connected by different types of hedgerows and surrounded by a less disturbed matrix with fewer and smaller crop fields (see Valdés et al., 2015 for more info). In each landscape window, sixteen woodlands were selected for sampling. When possible, these woodlands were chosen to be equally distributed among each of four combinations of size and historical age categories: small-old, small-young, large-old, large-young (see details on patch selection in Appendix S1, and summary statistics for each size and age category per landscape window in Table S1).

## 2.2 | Data collection

### 2.2.1 | Patch features

Patch size and historical age were calculated with a geographic information system (GIS, ArcGIS 9.3, ESRI), using contemporary and historical maps of the landscape windows (recent aerial photographs, all taken after the year 2000, and maps from the 18th, 19th and 20th centuries). Patch size was calculated using digitized woodlands in each window. For calculating patch historical age, we digitized all woodlands in historical maps, and historical age was estimated using the date of the oldest map on which a patch appeared. As a given patch may contain a mosaic of fragments with different historical ages, we calculated a size-weighted average of the historical age of all fragments composing an isolated patch.

We used a 500-m buffer centred on each patch to calculate metrics related to habitat connectivity (see also Valdés et al., 2015) and the habitat amount hypothesis sensu Fahrig (2013): (a) the proportion of buffer surface covered by forest, with higher values indicating a higher amount of forest habitat availability within the landscape; and (b) the proportion of buffer surface covered by crops, with higher values indicating a lower habitat connectivity, as agricultural intensification of the matrix reduces forest connectivity and increases its ecological isolation (Donald & Evans, 2006).

### 2.2.2 | Environmental drivers

We calculated values of three groups of environmental drivers that can affect both biodiversity and supply potential of multiple ecosystem services: macroclimatic, soil and forest structural drivers.

#### *Macroclimatic drivers*

We extracted five temperature variables from the EuroLST dataset (250-m resolution, <http://www.geodati.fmach.it/eurolst.html>) and five precipitation variables from the WorldClim global database (1-km resolution, <http://www.worldclim.org/>) and averaged each variable for each patch using all pixels intersecting with the patch

area. We performed a principal components analysis (PCA, Figure S1) on these 10 variables representing seasonality and extreme or limiting environmental factors (see details on Figure S1 legend), and retained the first axis (explaining 74% of the total variance) as an explanatory variable in our models. This variable, called "macroclimate", indicated high seasonality and low temperature and precipitation.

#### *Soil drivers*

We took soil samples in each patch (see details on soil sampling in Appendix S1), and calculated mean values of depth of the forest floor, C:N ratio, total P content and pH of the mineral topsoil at the patch level and used them to perform a PCA (Figure S2). We then retained axes 1 and 2 (explaining, respectively, 44% and 26% of the total variance) as explanatory variables in our models. Axis 1, called 'soil nutrients', was positively correlated with the total P in the mineral topsoil and negatively correlated with the depth of the forest floor. Axis 2, called 'soil acidity & C/N' was positively correlated with the C:N ratio in the mineral topsoil and negatively correlated with the pH of the mineral topsoil.

#### *Forest structural drivers*

We calculated two variables describing variation in forest composition and structure, respectively: tree diversity, calculated as a stem number-based Shannon diversity index; and structural diversity, calculated as the coefficient of variation (CV) of tree diameters (see details on data collection in Appendix S1). These variables were selected based on data availability on the one hand and their relevance for explaining variation in tree and forest-associated biodiversity and in ecosystem functioning (e.g. van der Plas et al., 2016 and Penone et al., 2019) on the other hand.

### 2.2.3 | Biodiversity

In order to assess patch biodiversity (hereafter multidiversity sensu Allan et al., 2014), we surveyed species richness for six different taxonomic groups that are representative of forest-associated ground-dwelling biota: ground beetles (i.e. Insecta); spiders (i.e. Arachnida); millipedes (i.e. Myriapoda); woodlice (i.e. Crustacea); understory herbs (i.e. focusing on vascular plant species only); and mushrooms (i.e. focusing on species with visible and above-ground fruiting bodies such as stem, cap and gills). The selected groups cover different trophic levels (primary producers, predators and decomposers) and are assumed to directly or indirectly influence the potential delivery of the six studied ecosystem (dis) services. We refer to Appendix S1 for more information on field surveys specific to each taxonomic group.

### 2.2.4 | Proxies for supply potential of multiple ecosystem services

In addition to patch multidiversity, we assessed the potential of a given patch to simultaneously provide multiple services (hereafter

multiservice delivery potential). Here we included two proxies for provisioning services (abundance of usable plants and stemwood volume), three for regulating services (pest control potential, tick-borne disease risk and topsoil carbon storage), and one for a cultural or recreational service (game production potential). See Appendix S1 for more information on each service/disservice and details on data collection.

### 2.3 | Calculation of multidiversity and multiservice delivery

For each patch  $i$ , we calculated a multidiversity index (MD) according to Allan et al. (2014) using the raw species richness values of understory herbs (UH), mushrooms (MU), carabid beetles (CB), spiders (SP), millipedes (MI) and woodlice (WO). Each raw species richness value for a given taxonomic group was divided by the mean of the five highest values among all studied patches to account for extreme values (Allan et al., 2014). MD was calculated as:

$$\text{MD} = \text{average} \left[ \left( \frac{\text{UH}_i}{\text{UH}_{5\text{highest}}} + \frac{\text{MU}_i}{\text{MU}_{5\text{highest}}} + \frac{\text{CB}_i}{\text{CB}_{5\text{highest}}} + \frac{\text{SP}_i}{\text{SP}_{5\text{highest}}} + \frac{\text{MI}_i}{\text{MI}_{5\text{highest}}} + \frac{\text{WO}_i}{\text{WO}_{5\text{highest}}} \right) \right] \quad (1)$$

Based on the raw values of each individual ecosystem service/disservice, we used a multiple threshold approach (Byrnes et al., 2014) to define service-specific threshold values representing low, intermediate and high performance levels of ecosystem service supply potential (see details in Table S2). The performance level is the amount of the provided service (or disservice) supply potential per area unit and could either be low, intermediate or high. Examples of high performance levels are, for instance, small woodland patches that simultaneously provide a large total stemwood volume (>300 m<sup>3</sup> per ha) and have a low density of ticks (<50 nymphs per 100 m<sup>2</sup>) and thus minimize the prevalence of tick-borne diseases in the human population. For each of the three performance levels, we calculated multiservice delivery potential as the proportion of ecosystem service proxies (sometimes less than six measured ecosystem proxies per patch if the data was not available for a given proxy within a focal patch) for which the amount of the provided service (or disservice) proxy per area unit exceeded (or was lower than) a proxy-dependent threshold (Table S2). For instance, if one service proxy exceeded its high-threshold value and two exceeded their respective low-threshold values within a given patch for which five services were measured in total, then the high-performance multiservice delivery potential is 0.2 and the low-performance multiservice delivery is 0.4 for this patch. This threshold approach is considered as the state-of-the-art standard method to evaluate multiservice delivery (Byrnes et al., 2014; Gamfeldt, Hillebrand, & Jonsson, 2008; Lefcheck et al., 2015). Multiple thresholds are used because it has been shown that the sign of the relationship between biodiversity and ecosystem multifunctionality can differ when low-performance versus high-performance thresholds are applied (van der Plas et al., 2016).

### 2.4 | Statistical modelling

We used piecewise structural equation modeling (piecewise SEM, Lefcheck, 2016) to study the response of low-, intermediate- and high-performance multiservice delivery potential to multidiversity, patch characteristics (size, age and the interaction between size and age) as well as habitat availability and connectivity within the landscape, while accounting also for macroclimate, soil and forest structural characteristics. We chose a piecewise approach (instead of the traditional variance-covariance-based SEM) because of its ability to fit multiple separate linear models with non-normal distributions and random effects, which was well-suited for our data. In our models, we considered both direct responses of multiservice delivery potential to the different predictors, and indirect responses mediated by effects of the different predictors on multidiversity. The piecewise SEM consisted of four component models:

1. A linear mixed-effects model (LMM) with tree diversity as the response variable and patch size (log-transformed), historical age, habitat availability (proportion of forests) and connectivity (proportion of crops), macroclimate (PC1) and soil (PC1 and PC2) as predictor variables.
2. A LMM with structural diversity as the response variable and patch size (log-transformed), historical age, habitat availability (proportion of forests) and connectivity (proportion of crops) and tree diversity as predictor variables.
3. A LMM with multidiversity as the response variable and patch size (log-transformed), historical age (and their interaction term to account for the species-time-area relationship; Adler et al., 2005), habitat availability (proportion of forests) and connectivity (proportion of crops), macroclimate (PC1), soil (PC1 and PC2), tree diversity and structural diversity as predictor variables.
4. A generalized linear mixed-effects model (GLMM) with a binomial error distribution with multiservice delivery potential as the response variable and multidiversity, patch size (log-transformed), historical age, habitat availability (proportion of forests) and connectivity (proportion of crops), macroclimate (PC1), soil (PC1 and PC2), tree diversity and structural diversity as predictor variables.

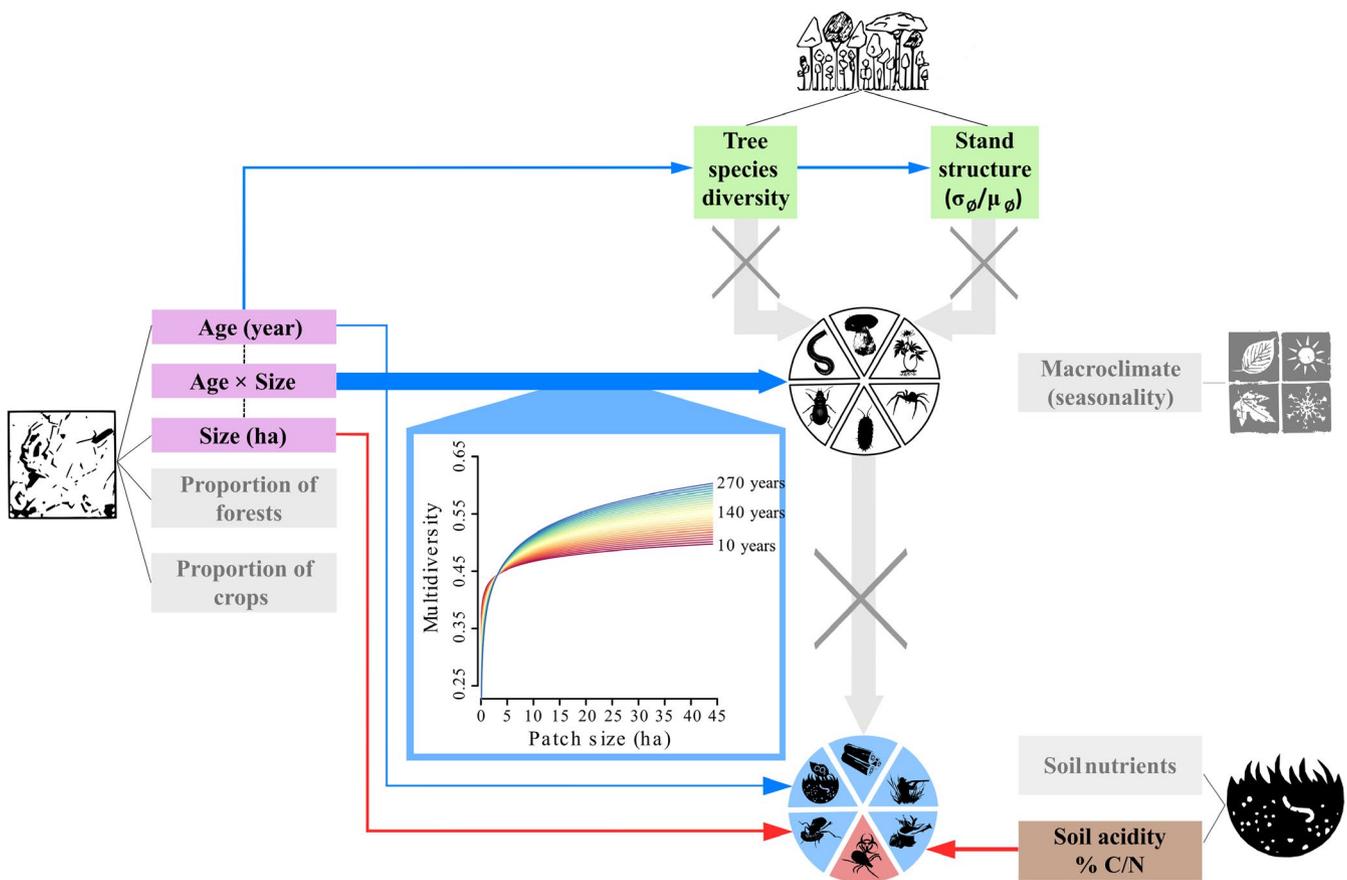
LMMs were used for response variables with approximately normal distributions (tree diversity, structural diversity and multidiversity), and a binomial GLMM was used for multiservice delivery potential (proportional). We used 'region' and 'window type' nested within 'region' as random effect terms in all

four component models to account for the hierarchical, nested structure of the sampling design along the studied gradient. This piecewise SEM model structure was tested for the three levels of performance of multiservice delivery potential considered (low, intermediate and high), and for each individual ecosystem service, separately. Overall fit of the piecewise SEM models was assessed using Shipley's test of direct separation (Shipley, 2009), which evaluates the probability that none of the paths missing from the hypothesized causal network contain useful information, and yields the Fisher's C statistic. A  $\chi^2$ -value of Fisher's C below the significance level ( $p < .05$ ) indicates that the model is inconsistent with the data, and should be rejected. Statistical analyses were carried out in R 3.4.2 (R Core Team, 2018) using the packages piecewiseSEM (Lefcheck, 2016) and nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2016).

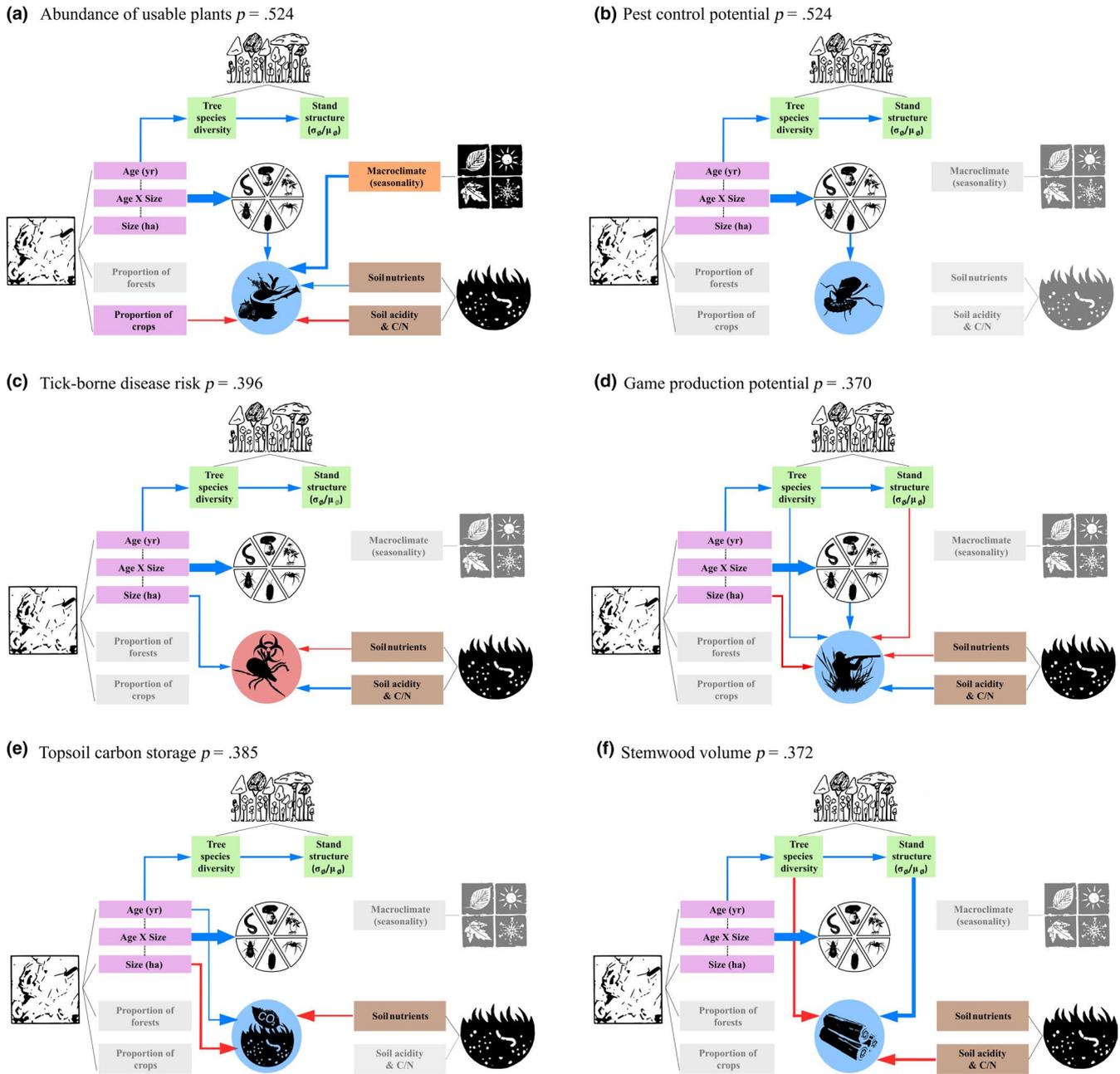
### 3 | RESULTS

Tree species diversity increased with patch historical age, while structural diversity, in turn, increased with tree species diversity (Figure 3). Multidiversity was higher in the larger and more ancient patches, as shown by the positive interaction effect ( $p = .03$ ) between patch size and historical age (Figure 3).

The response of multiservice delivery potential to multidiversity, patch characteristics, habitat availability and connectivity and environmental drivers depended on the level of performance considered. Multiservice delivery potential at a low performance level increased with multidiversity and was also indirectly positively affected by the interaction between patch size and historical age as larger and more ancient patches hosted higher levels of multidiversity (Figure S3). Multiservice delivery potential at an intermediate performance



**FIGURE 3** Linkage between the environment, biodiversity and high-performance multiservice delivery potential in small woodlands across Europe. Results of the piecewise structural equation model ( $p = .512$ ) studying the response of high-performance multiservice delivery potential to multidiversity, patch size, age and connectivity (proportion of forests and crops in a 500-m surface around each patch), while accounting for macroclimate, soil and forest structural characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only significant paths ( $p < .05$ ) are shown, while variables not significantly contributing to the models are attenuated and represented with grey shading. Grey crossed arrows have been included to highlight the lack of effects of multidiversity on multiservice, and of tree species diversity and stand structure on multidiversity. The blue square depicts the positive interaction effect ( $p = .03$ ) between patch size and historical age on multidiversity, as predicted by the species–time–area relationship. Marginal (i.e. fixed effects) and conditional (fixed plus random effects)  $R^2$  values are .33 and .48, respectively. The colour ramp from red to blue depicts different historical patch ages ranging from the youngest (10 years) to the oldest (270 years) sampled patch ( $n = 200$ ). All covariates (connectivity, macroclimate, soil and stand conditions) in the model except patch size and historical age were set to their mean values



**FIGURE 4** Linkage between the environment, biodiversity and individual ecosystem service supply potential in small woodlands across Europe. Results of the piecewise structural equation models studying the response of each individual ecosystem service to multidiversity, patch size, historical age and connectivity (proportion of forests and crops in a 500-m surface around each patch), while accounting also for macroclimate, soil and forest structural characteristics as environmental drivers. Blue arrows indicate positive effects and red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only significant paths ( $p < .05$ ) are shown, while variables not significantly contributing to the models are attenuated and represented with grey shading. The overall  $p$ -value for each piecewise structural equation model (piecewise SEM) is shown in the heading of each panel

level was not affected by any of the studied drivers (Figure S3). Multiservice delivery potential at a high performance level increased directly with patch historical age and decreased directly with patch size, i.e. it was maximal in the smallest and most ancient woodlands (Figure 3). It also decreased with soil acidity and C/N, that is it was maximal in less acidic soils with lower C:N ratio (Figure 3).

Each individual ecosystem service/disservice showed a particular response to the array of drivers studied (Figure 4). Patch size

affected three ecosystem service proxies and patch age only one. Smaller woodlands exhibited a higher game production potential and topsoil carbon storage capacity, but lower tick-borne disease risk than larger patches. More ancient woodlands showed a higher topsoil carbon storage. Multidiversity, mediated by the positive interaction effect of patch size  $\times$  patch age, had a significant positive impact on three out of the six individual ecosystem services studied: abundance of usable plants, pest control potential and game

production potential, while tick-borne disease risk, topsoil carbon storage, and stemwood volume were unaffected by multidiversity. The landscape variables only had a limited effect on the ecosystem service delivery potential, with only the abundance of usable plants positively related to habitat connectivity. The abundance of usable plants was also the only service proxy affected by macroclimate; enhanced seasonality had a positive effect. Soil drivers affected several individual ecosystem services. Soil nutrient availability increased the abundance of usable plants and decreased tick-borne disease risk, game production potential and topsoil carbon storage. Tick-borne disease risk and game production potential increased in more acidic soils with higher C:N ratio, while the abundance of usable plants and stemwood volume decreased. Forest structure affected two proxies: game production potential increased with tree species diversity and decreased with structural diversity, and stemwood volume, which decreased with tree species diversity and increased with structural diversity. All piecewise SEM models reported here were consistent with the data ( $p > .05$  in all cases).

## 4 | DISCUSSION

We showed that multidiversity was highest in large and ancient forest patches. Multiservice delivery potential at high performance levels per area was maximal in the smallest and most ancient woodlands and was not affected by multidiversity, which only influenced multiservice delivery potential at low performance levels, as well as some of the individual ecosystem services.

### 4.1 | The interplay between patch biodiversity, age and size and their effects on multiservice delivery potential

Our results show that, although larger and more ancient woodlands hosted a higher biodiversity, as predicted by the species-time-area relationship (Adler et al., 2005), this was unrelated to a high-performance multiservice delivery potential. Contrary to our expectations, high-performance multiservice delivery potential decreased as patch size increased, independent of the positive effect of patch size on multidiversity. This means that smaller woodlands potentially deliver multiple services at higher performance levels on a per area basis than larger woodlands of a similar age, even if the larger woodlands harbor a higher biodiversity. This unexpected result may be explained by the positive edge effect on the delivery potential of some ecosystem services (Bodin et al., 2006; Mitchell et al., 2014). As smaller woodlands have a relatively high edge-to-core ratio (Ewers & Banks-Leite, 2013; Weathers, Cadenasso, & Pickett, 2001), they are highly exposed to external influences; they receive, for example, proportionally more light penetrating through the edge, a warmer and drier microclimate and more nutrient input from surrounding agricultural lands compared to large forests. These conditions promote, among others,

higher patch-level microclimate heterogeneity (Frey et al., 2016) as well as a more dense vegetation cover and an increased biomass production at forest edges (Remy, Wuyts, Van Nevel, et al., 2018; Remy, Wuyts, Verheyen, Gundersen, & Boeckx, 2018) in small woodlands. This altered functioning in turn increases the delivery potential of some services, such as game production potential, due to an increased quantity of food available for game, and topsoil carbon storage, due to the faster incorporation of organic matter in the soil. Tick-borne disease risk is, however, lower, likely due to decreased larval densities in the unfavourable (e.g. hotter and drier) microclimatic conditions at the edge (Ehrmann et al., 2017).

On the other hand, the positive and indirect interaction effect of patch size and age, mediated by a higher multidiversity, increased multiservice delivery potential at a low-performance level, as well as some individual ecosystem services. Therefore, it seems that the higher biodiversity hosted by larger and more ancient woodlands is able to maintain a minimal level of multiservice supply potential, while the maintenance of higher levels is less dependent on the amount of biodiversity. The supply potential of several individual ecosystem services indirectly increased in larger and more ancient woodlands because it was dependent on higher levels of biodiversity. For example, abundance of usable plants and game production potential might have increased due to a positive correlation with vascular plant diversity, while pest control potential probably increased due to bottom-up effects through the trophic chain (Scherber et al., 2010). On the contrary, tick-borne disease risk, topsoil carbon storage and stemwood volume were unrelated to multidiversity, probably because they depended on particular environmental conditions or on the presence and abundance of specific species (Winfree, Fox, Williams, Reilly, & Cariveau, 2015) rather than on species richness per se.

Finally, it should be noted that we focused on the service delivery potential on a per area basis and that the total amount of services provided by large patches might still be larger than that of small patches. Our findings should therefore not be interpreted as a trade-off between large, biodiverse patches versus small patches that have a higher potential to deliver services, but rather as an observation that small woodlands in agricultural landscapes have the potential to deliver a high flow of services relative to their size.

### 4.2 | The effect of other drivers on woodland multiservice delivery potential

The amount of forest cover around each woodland (cf. the habitat amount hypothesis, Fahrig, 2013) had no effect on multidiversity, multiservice delivery potential and individual services, which indicates that habitat availability within the landscape did not influence the service supply potential. This lack of effect may be a consequence of the disruption of metacommunity functioning in highly fragmented

systems, with the dispersal of species among small forest patches dramatically reduced (Jamoneau, Chabrierie, Closset-Kopp, & Decocq, 2012). Both models (Thompson & Gonzalez, 2016) and experiments (Haddad et al., 2015) predict reduced multifunctionality in such highly fragmented systems. The delivery of some ecosystem services may decline with low habitat connectivity, and with an intensively managed landscape matrix, as we have observed for the abundance of usable plants, which decreased with the proportion of crops surrounding the forest patch. Such an effect most likely results from a greater exposure of the forest edges to the biocides and fertilizers used in the adjacent croplands (Chabrierie, Jamoneau, Gallet-Moron, & Decocq, 2013).

Macroclimatic conditions affected neither multidiversity nor multiservice delivery potential, although we studied a large climatic gradient covering the entire European temperate biome. Only one of the individual services, the abundance of usable plants, was positively affected by macroclimate seasonality, increasing towards northern latitudes. This overall lack of effects of macroclimate suggests that the expected major biogeographic gradients influencing ecosystem service delivery potential are lost in highly fragmented forest ecosystems, at least partly due to the loss of macroclimate-driven biodiversity gradients (Valdés et al., 2015; Vanneste et al., 2019) and a decoupling between sub-canopy and free-air temperatures (De Frenne et al., 2013, 2019; Frey et al., 2016; Lenoir, Hattab, & Pierre, 2017). Similarly, other potentially influential microclimate factors such as soil moisture and relative air humidity, not assessed in this study, could contribute to the observed lack of effects of macroclimate on multidiversity and multiservice delivery.

### 4.3 | Future research avenues

This study is a first step towards a better understanding of the factors that influence the biodiversity and multiservice delivery potential of woodland patches in agricultural landscapes. Obviously, not all possible services were considered here (see Decocq et al., 2016 for an overview) and this raises the question of whether inclusion of other services, like erosion control and water quality regulation, both acting at a landscape scale, would alter the results. This is not unlikely, since it has been shown that different services are underpinned by different forest attributes (Felipe-Lucia et al., 2018). Next, inclusion of more driving variables, e.g. those that quantify the past and current management and the microclimate in the patches, may help to further clarify how human actions in these patches influence their biodiversity and ecosystem service delivery potential. Another research avenue along the same lines is making the step from ecosystem service delivery potential towards actual ecosystem delivery. Indeed, not all services play an equally important role in all landscapes or for all stakeholders, and potential ecosystem service assessments should ideally be complemented by socio-economic analyses quantifying the importance and value of the studied services (e.g. Bagstad et al., 2014; Zoderer, Tasser, Carver, & Tappeiner, 2019). Finally, such integrated analyses will require

the use of more sophisticated indicators that better reflect the actual ecosystem services that are delivered than the indicators we used.

## 5 | CONCLUSIONS

Our study responds to the call for empirical research into the nature of the relationships between fragmentation and ecosystem service supply potential (Mitchell et al., 2015). We have shown that both large and small woodland patches in agricultural landscapes fulfill important roles. The large, ancient woodlands host the highest biodiversity and are particularly important for conservation. They also have the potential to deliver a considerable flow of services, but smaller woodlands have a higher potential to deliver multiple ecosystem services on a per area basis than the larger woodlands, especially when they are ancient. This higher potential of small woodlands might be caused by edge effects that can enhance the delivery potential of several services. Preserving the small woodlands is hence important to increase the multifunctionality of agricultural landscapes. This is an important finding because especially the small woodlands are currently not included in major national and international policies affecting biodiversity and ecosystem services in agricultural landscapes, such as the EU Natura 2000 network, the EU water Directive and the Common Agricultural Policy (Pe'er et al., 2014). Our findings advocate for the development of relevant policy instruments in order to ensure their future conservation. Next, we also found that the importance of drivers vary depending on performance levels of the ecosystem service and on the individual (dis-)service considered. A given driver may thus affect individual services in opposite directions, which leads to trade-offs among services (Felipe-Lucia et al., 2018; Gamfeldt et al., 2013; Lefcheck et al., 2015). Consequently, different management strategies of these woodlands would be required to achieve multiservice delivery at high performance levels or to maximize (respectively minimize) the delivery of a specific ecosystem service (respectively disservice). For some services and performance levels, biodiversity conservation and ecosystem service delivery go hand in hand, but in other cases there may be a trade-off between both. This should be taken into account when designing policies and management strategies for small woodlands in agricultural landscapes.

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## AUTHORS' CONTRIBUTIONS

A.V., J.L. and P.D.F. contributed equally to the work. K.V. and G.D. share the last authorship. A.V., J.L., P.D.F., K.V. and G.D. designed the study. All authors collected the data. J.L., A.V., P.D.F. and K.V. analyzed the data. A.V., J.L., P.D.F., K.V. and G.D. wrote the first draft of the paper. All authors contributed substantially to the writing and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.cfxpvnv2c> (Valdés et al., 2019).

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## REFERENCES

- Adler, P. B., White, E. P., Lauenroth, W. K., Kaufman, D. M., Rassweiler, A., & Rusak, J. A. (2005). Evidence for a general species-time-area relationship. *Ecology*, 86(8), 2032–2039. <https://doi.org/10.1890/05-0067>
- Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tschamtko, T., ... Fischer, M. (2014). Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 111(1), 308–313. <https://doi.org/10.1073/pnas.1312213111>
- Bagstad, K., Villa, F., Batker, D., Harrison-Cox, J., Voigt, B., & Johnson, G. (2014). From theoretical to actual ecosystem services: mapping beneficiaries and spatial flows in ecosystem service assessments. *Ecology and Society*, 19(2). <https://doi.org/10.5751/ES-06523-190264>
- Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9(10), 1146–1156. <https://doi.org/10.1111/j.1461-0248.2006.00963.x>
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., ... Griffin, J. N. (2013). Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *BioScience*, 64(1), 49–57. <https://doi.org/10.1093/biosci/bit003>
- Bastian, O. (2013). The role of biodiversity in supporting ecosystem services in Natura 2000 sites. *Ecological Indicators*, 24(1), 12–22. <https://doi.org/10.1016/j.ecolind.2012.05.016>
- Bodin, Ö., Tengö, M., Norman, A., Lundberg, J., & Elmqvist, T. (2006). The value of small size: Loss of forest patches and ecological thresholds in Southern Madagascar. *Ecological Applications*, 16(2), 440–451. [https://doi.org/10.1890/1051-0761\(2006\)016\[0440:TVOSSL\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0440:TVOSSL]2.0.CO;2)
- Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., ... Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, 5(2), 111–124. <https://doi.org/10.1111/2041-210X.12143>
- Chabrierie, O., Jamoneau, A., Gallet-Moron, E., & Decocq, G. (2013). Maturation of forest edges is constrained by neighbouring agricultural land management. *Journal of Vegetation Science*, 24(1), 58–69. <https://doi.org/10.1111/j.1654-1103.2012.01449.x>
- Craven, D., Filotas, E., Angers, V. A., & Messier, C. (2016). Evaluating resilience of tree communities in fragmented landscapes: Linking functional response diversity with landscape connectivity. *Diversity and Distributions*, 22(5), 505–518. <https://doi.org/10.1111/ddi.12423>
- De Frenne, P., Baeten, L., Graae, B. J., Brunet, J., Wulf, M., Orczewska, A., ... Verheyen, K. (2011). Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, 99(2), 600–609. <https://doi.org/10.1111/j.1365-2745.2010.01768.x>
- De Frenne, P., Rodriguez-Sanchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., ... Verheyen, K. (2013). Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 110(46), 18561–18565. <https://doi.org/10.1073/pnas.1311190110>
- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3(5), 744–749. <https://doi.org/10.1038/s41559-019-0842-1>
- Decocq, G., Andrieu, E., Brunet, J., Chabrierie, O., De Frenne, P., De Smedt, P., ... Wulf, M. (2016). Ecosystem services from small forest patches in agricultural landscapes. *Current Forestry Reports*, 2(1), 30–44. <https://doi.org/10.1007/s40725-016-0028-x>
- Donald, P. F., & Evans, A. D. (2006). Habitat connectivity and matrix restoration: The wider implications of agri-environment schemes. *Journal of Applied Ecology*, 43(2), 209–218. <https://doi.org/10.1111/j.1365-2664.2006.01146.x>
- Duffy, J. E., Godwin, C. M., & Cardinale, B. J. (2017). Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549(7671), 261–264. <https://doi.org/10.1038/nature23886>
- Ehrmann, S., Liira, J., Gärtner, S., Hansen, K., Brunet, J., Cousins, S. A. O., ... Scherer-Lorenzen, M. (2017). Environmental drivers of *Ixodes ricinus* abundance in forest fragments of rural European landscapes. *BMC Ecology*, 17(1). <https://doi.org/10.1186/s12898-017-0141-0>
- Estreguil, C., Caudullo, G., de Rigo, D., & San Miguel, J. (2013). Forest landscape in Europe: pattern, fragmentation and connectivity. *EUR Scientific and Technical Research*, 25717. Retrieved from [http://vwbxforest.jrc.it/media/cms\\_page\\_media/53/2012-fragmentation\\_executive%20rep\\_EUR25717.doc.pdf](http://vwbxforest.jrc.it/media/cms_page_media/53/2012-fragmentation_executive%20rep_EUR25717.doc.pdf)
- Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS ONE*, 8(3), e58093. <https://doi.org/10.1371/journal.pone.0058093>
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40(9), 1649–1663. <https://doi.org/10.1111/jbi.12130>
- Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., ... Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, 9(1), 4839. <https://doi.org/10.1038/s41467-018-07082-4>
- Flinn, K. M., & Vellend, M. (2005). Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, 3(5), 243–250. [https://doi.org/10.1890/1540-9295\(2005\)003\[0243:ROFPCI\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0243:ROFPCI]2.0.CO;2)
- Frey, S. J., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of old-growth forests. *Science Advances*, 2(4), e1501392. <https://doi.org/10.1126/sciadv.1501392>

- Gamfeldt, L., Hillebrand, H., & Jonsson, P. R. (2008). Multiple functions increase the abundance of biodiversity for overall ecosystem functioning. *Ecology*, 89(5), 1223–1231. <https://doi.org/10.1890/06-2091.1>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., ... Bengtsson, J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, 4, 1340. <https://doi.org/10.1038/ncomms2328>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2), e1500052–e1500052. <https://doi.org/10.1126/sciadv.1500052>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Loveland, T. R. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853.
- Herrera, J. M., & García, D. (2009). The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation*, 142(1), 149–158. <https://doi.org/10.1016/j.biocon.2008.10.008>
- Hunter, M. L. (2017). Conserving small natural features with large ecological roles: An introduction and definition. *Biological Conservation*, 211, 1–2. <https://doi.org/10.1016/j.biocon.2016.12.019>
- Jamoneau, A., Chabrierie, O., Closset-Kopp, D., & Decocq, G. (2012). Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography*, 35(2), 124–133. <https://doi.org/10.1111/j.1600-0587.2011.06900.x>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Lefcheck, J. S., Byrnes, J. E. K., Isbell, F., Gamfeldt, L., Griffin, J. N., Eisenhauer, N., ... Duffy, J. E. (2015). Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nature Communications*, 6, 6936. <https://doi.org/10.1038/ncomms7936>
- Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: Implications for species redistribution. *Ecography*, 40(2), 253–266. <https://doi.org/10.1111/ecog.02788>
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, 132(3), 311–321. <https://doi.org/10.1016/j.biocon.2006.04.023>
- Manning, A. D., Gibbons, P., & Lindenmayer, D. B. (2009). Scattered trees: A complementary strategy for facilitating adaptive responses to climate change in modified landscapes? *Journal of Applied Ecology*, 46(4), 915–919. <https://doi.org/10.1111/j.1365-2664.2009.01657.x>
- Mitchell, M. G. E., Bennett, E. M., & Gonzalez, A. (2014). Forest fragments modulate the provision of multiple ecosystem services. *Journal of Applied Ecology*, 51(4), 909–918. <https://doi.org/10.1111/1365-2664.12241>
- Mitchell, M. G. E., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., ... Rhodes, J. R. (2015). Reframing landscape fragmentation's effects on ecosystem services. *Trends in Ecology & Evolution*, 30(4), 190–198. <https://doi.org/10.1016/j.tree.2015.01.011>
- Naaf, T., & Kolk, J. (2015). Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biological Conservation*, 182, 155–163. <https://doi.org/10.1016/j.biocon.2014.12.002>
- Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Baldi, A., Benton, T. G., ... Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, 344(6188), 1090–1092. <https://doi.org/10.1126/science.1253425>
- Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., ... Fischer, M. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecology Letters*, 22(1), 170–180. <https://doi.org/10.1111/ele.13182>
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2016). *nlme: Linear and nonlinear mixed effects models. R package version 3.1-128*.
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>
- Remy, E., Wuyts, K., Van Nevel, L., De Smedt, P., Boeckx, P., & Verheyen, K. (2018). Driving factors behind litter decomposition and nutrient release at temperate forest edges. *Ecosystems*, 21(4), 755–771. <https://doi.org/10.1007/s10021-017-0182-4>
- Remy, E., Wuyts, K., Verheyen, K., Gundersen, P., & Boeckx, P. (2018). Altered microbial communities and nitrogen availability in temperate forest edges. *Soil Biology and Biochemistry*, 116, 179–188. <https://doi.org/10.1016/j.soilbio.2017.10.016>
- Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., ... Tscharrntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323), 553–556. <https://doi.org/10.1038/nature09492>
- Shipley, B. (2009). Confirmatory path analysis in a generalized multi-level context. *Ecology*, 90(2), 363–368. <https://doi.org/10.1890/08-1034.1>
- Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5), 1125–1140. <https://doi.org/10.1111/j.1365-2486.2008.01557.x>
- Thompson, P. L., & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97(10), 2867–2879. <https://doi.org/10.1002/ecy.1502>
- Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrierie, O., ... Decocq, G. (2019). Data from: High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.cfxpvnv2c>
- Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., ... Decocq, G. (2015). The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Global Ecology and Biogeography*, 24(9), 1094–1105. <https://doi.org/10.1111/geb.12345>
- van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., ... Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature Communications*, 7, 11109. <https://doi.org/10.1038/ncomms11109>
- Vanneste, T., Valdés, A., Verheyen, K., Perring, M. P., Bernhardt-Römermann, M., Andrieu, E., ... De Frenne, P. (2019). Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, 34, 1–14. <https://doi.org/10.1016/j.bae.2018.09.004>
- Weathers, K. C., Cadenasso, M. L., & Pickett, S. T. A. (2001). Forest edges as nutrient and pollutant concentrators: Potential synergisms between fragmentation, forest canopies and the atmosphere. *Conservation Biology*, 15(6), 1506–1514. <https://doi.org/10.1046/j.1523-1739.2001.01090.x>
- Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, 18(7), 626–635. <https://doi.org/10.1111/ele.12424>
- Zoderer, B. M., Tasser, E., Carver, S., & Tappeiner, U. (2019). Stakeholder perspectives on ecosystem service supply and ecosystem

service demand bundles. *Ecosystem Services*, 37, 100938. <https://doi.org/10.1016/j.ecoser.2019.100938>

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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