High ecosystem service delivery potential of small woodlands in agricultural landscapes

Alicia Valdés, Jonathan Roger Michel Henri Lenoir, Pieter de Frenne, Emilie Andrieu, Jorg Brunet, Olivier Chabrerie, Sara A. O. Cousins, Marc Deconchat, Pallieter de Smedt, Martin Diekmann, et al.

To cite this version:

Alicia Valdés, Jonathan Roger Michel Henri Lenoir, Pieter de Frenne, Emilie Andrieu, Jorg Brunet, et al.. High ecosystem service delivery potential of small woodlands in agricultural landscapes. Journal of Applied Ecology, 2020, 57 (1), pp.4-16. 10.1111/1365-2664.13537 . hal-02618817

HAL Id: hal-02618817
https://hal.inrae.fr/hal-02618817v1

Submitted on 10 Nov 2020

TITLE: "Small but strong: High ecosystem service delivery potential of small woodlands in agricultural landscapes"

AUTHOR LIST: Alicia Valdés[1*†], Jonathan Lenoir[1*], Pieter De Frenne[2*], Emilie Andrieu[3], Jörg Brunet[4], Olivier Chabrerie[1], Sara A. O. Cousins[5], Marc Deconchat[3], Pallieter De Smedt[2], Martin Diekmann[6], Steffen Ehrmann[7], Emilie Gallet-Moron[1], Stefanie Gärtner[7], Brice Giffard[3], Karin Hansen[8], Martin Hermy[9], Annette Kolb[6], Vincent Le Roux[1], Jaan Liira[10], Jessica Lindgren[5], Ludmilla Martin[1], Tobias Naaf[11], Taavi Paal[10], Willem Proesmans[2], Michael Scherer-Lorenzen[7], Monika Wulf[11], Kris Verheyen[2**], Guillaume Decocq[1**].

[*]These authors contributed equally to the work

[**]Shared last authorship

[†]Corresponding author, e-mail: aliciavaldes1501@gmail.com, present affiliations: Department of Ecology, Environment and Plant Sciences, Stockholm University, Svante Arrhenius väg 20 A, SE-106 91 Stockholm, Sweden & Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

Author affiliations:

[1]"Ecologie et Dynamique des Systèmes Anthropisés" (EDYSAN, UMR CNRS 7058), Jules Verne University of Picardie, 1 rue des Louvels, F-80037 Amiens Cedex 1, France, [2]Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Belgium, [3]UMR 1201 DYNAFOR, INRA, Chemin de Borde Rouge, CS 52627 F-31326 Castanet, France, [4]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Box 49, SE-230 53 Alnarp, Sweden, [5]Landscape Ecology, Department of Geography and Quaternary Geology, Stockholm University, SE-106 91 Stockholm, Sweden, [6]Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Strasse, D-28359 Bremen, Germany, [7]Chair of Geobotany,

Faculty of Biology, University of Freiburg, Schaenzlestrasse 1, 79104 Freiburg, Germany,

[8]IVL Swedish Environmental Research Institute, Box 210 60, S-100 31 Stockholm, Sweden,

[9]Division Forest, Nature and Landscape Research, University of Leuven (KU Leuven), Celestijnenlaan 200E, B-3000 Leuven, Belgium, [10]Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia, [11]Leibniz-ZALF (e.V.), Institute of Land Use Systems, Eberswalder Strasse 84, D-15374 Müncheberg, Germany.

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 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*: Though large, ancient woodlands host the highest biodiversity and hence, can deliver a number of ecosystem services, 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, these small woodlands are currently not considered by public policies. There is thus an urgent need for targeted policy instruments ensuring 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: Anthropocene, biodiversity, connectivity, habitat fragmentation, island biogeography, management practices, metacommunity dynamics, multifunctionality, woodlands

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 (Fig. 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 or functional diversity on ecosystem functioning and service delivery is widely acknowledged and very well documented in the scientific literature (Balvanera et al., 2006; Balvanera et al., 2013; Bastian 2013; Gamfeldt et al., 2013; Lefcheck et al., 2015; van der Plas et al., 2016; Duffy, Godwin, & Cardinale, 2017). 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, Godwin, & Cardinale, 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; van der Plas et al., 2016; Lefcheck et al., 2015). 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 Fig. 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 Fig. 1).

Here, we assess 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 2500-km latitudinal gradient spanning the entire temperate forest biome in Europe (Fig. 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.

MATERIALS AND METHODS

Study area and sampling design

We studied deciduous forest patches in seven regions along a transect spanning *c*. 2500 km across the entire temperate forest biome of Europe (Fig. 2). In each region, two 5 × 5 km² landscape windows (14 in total) with two contrasting connectivity levels were selected: (1) 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 (2) 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).

Data collection

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 centered on each patch to calculate metrics related to habitat connectivity (see also Valdes et al., 2015) and the habitat amount hypothesis *sensu* Fahrig

(Fahrig, 2013): (1) the proportion of buffer surface covered by forest, with higher values indicating a higher amount of forest habitat availability within the landscape; and (2) 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).

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, Fig. S1) on these 10 variables representing seasonality and extreme or limiting environmental factors (see details on Fig. 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 (Fig. 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.

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 services. We refer to Appendix S1 for more information on field surveys specific to each taxonomic group.

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.

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:

$$MD = average\left[\left(\frac{UH_i}{UH^{-}_{5\,highest}} + \frac{MU_i}{MU^{-}_{5\,highest}} + \frac{CB_i}{CB^{-}_{5\,highest}} + \frac{SP_i}{SP^{-}_{5\,highest}} + \frac{MI_i}{MI^{-}_{5\,highest}} + \frac{WO_i}{WO^{-}_{5\,highest}}\right)\right]$$

(Equation 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^3 per ha) and have a low density of ticks (< 50 nymphs per 100 m^2) 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).

Statistical modeling

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 χ^2-value of Fisher's C below the significance level ($p < 0.05$) 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).

RESULTS

Tree species diversity increased with patch historical age, while structural diversity, in turn, increased with tree species diversity (Fig. 3). Multidiversity was higher in the larger and more ancient patches, as shown by the positive interaction effect ($p = 0.03$) between patch size and historical age (Fig. 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 (Fig. S3). Multiservice delivery potential at an intermediate performance level was not affected by any of the studied drivers (Fig. 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 (Fig. 3). It also decreased with soil acidity & C/N, i.e. it was maximal in less acidic soils with lower C:N ratio (Fig. 3).

Each individual ecosystem service/disservice showed a particular response to the array of drivers studied (Fig. 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 × 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 ($p > 0.05$ in all cases).

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.

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 unfavorable (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.

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, Chabrerie, 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 (Chabrerie, 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.

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 et al., 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.

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 (Gamfeldt et al., 2013; Lefcheck et al., 2015; Felipe-Lucia et al., 2018). 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.

AUTHORS' CONTRIBUTIONS

Author contributions: AV, JL and PDF contributed equally to the work. KV and GD share the last authorship. AV, JL, PDF, KV and GD designed the study. All authors collected the data. JL, AV, PDF and KV analyzed the data. AV, JL, PDF, KV and GD wrote the first draft of the paper. All authors contributed substantially to the writing and gave final approval for publication.

ACKNOWLEDGEMENTS

We acknowledge Catherine Bataillon, Déborah Closset-Kopp, Katharina Filzen, Kent Hansson, Aurélien Jamoneau, Tom Macheleidt, Willem Proesmans, Laurent Raison, Robert Saguez, Ilka Strubelt, Johan Van Keer, Rieneke Vanhulle, Stephan Wehling, Jérôme Willm and Christina Wolterink for fieldwork, Filip Moldan, Luc Willems, Greet de Bruyn and Lars Rosenqvist for help with soil analyses, Régis Courtecuisse and Pierre-Arthur Moreau for help with mushroom identification, Jérôme Buridant for help with patch history, Justine Louvel for database elaboration, Peter Manning for comments on an earlier version of the manuscript and Margot Vanhellemont for checking the English language. Funding: This research was funded by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG (Germany), BELSPO (Belgium) and DLR (Germany) part of the 2011 BiodivERsA call for research proposals.

DATA ACCESSIBILITY

Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository (e.g. Dryad) and the data DOI will be included at the end of the article.

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. doi: 10.1890/05-0067

Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M. M., Tscharntke, T., … Fischer, M. (2014). Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences*, *111*(1), 308–313. doi: 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). doi: 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. doi: 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. *BioScienc*e, *64*(1), 49–57. doi: 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. doi: 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. doi: 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. doi: 10.1111/2041-210X.12143

Chabrerie, 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. doi: 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. doi: 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. doi: 10.1111/j.1365-2745.2010.01768.x

De Frenne, P., Rodríguez-Sánchez, 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*, *110*(46), 18561–18565. doi: 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. doi: 10.1038/s41559-019-0842-1

Decocq, G., Andrieu, E., Brunet, J., Chabrerie, O., Frenne, P. D., Smedt, P. D., … Wulf, M. (2016). Ecosystem services from small forest patches in agricultural landscapes. *Current Forestry Reports*, *2*(1), 30–44. doi: 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. doi: 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. doi: 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). doi: 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://vwb-xforest.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. doi: 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. doi: 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. doi: 10.1146/annurev-ecolsys-110316-022612

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., Plas, F. van der, Boch, S., … Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, *9*(1), 4839. doi: 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.

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.

Gamfeldt, L., Hillebrand, H., & Jonsson, P. R. (2008). Multiple functions increase the abundance of biodiversity for overall ecosystem functioning. *Ecology*, *89*(5), 1223–1231. doi: 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. doi: 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. doi: 10.1126/sciadv.1500052

Hall, S. J. G., & Bunce, R. G. H. (2011). Mature trees as keystone structures in Holarctic ecosystems – a quantitative species comparison in a northern English park. *Plant Ecology & Diversity*, *4*(2–3), 243–250. doi: 10.1080/17550874.2011.586735

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.

Hunter, M. L. (2017). Conserving small natural features with large ecological roles: An introduction and definition. *Biological Conservation*, *211*, 1–2. doi: 10.1016/j.biocon.2016.12.019

Jamoneau, A., Chabrerie, O., Closset-Kopp, D., & Decocq, G. (2012). Fragmentation alters beta-diversity patterns of habitat specialists within forest metacommunities. *Ecography*, *35*(2), 124–133. doi: 10.1111/j.1600-0587.2011.06900.x

Jonsell, M. (2012). Old park trees as habitat for saproxylic beetle species. *Biodiversity and Conservation*, *21*(3), 619–642. doi: 10.1007/s10531-011-0203-0

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. doi: 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. doi: 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. doi: 10.1111/ecog.02788

Lindenmayer, D. B. (2017). Conserving large old trees as small natural features. *Biological Conservation*, *211*, 51–59. doi: 10.1016/j.biocon.2016.11.012

MacArthur, R. H., & Wilson, E. O. (1967). The theory of island biography. *Princeton, New Jersey*.

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.

Manning, Adrian D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures – Implications for conservation. *Biological Conservation*, *132*(3), 311–321. doi: 10.1016/j.biocon.2006.04.023

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. doi: 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*. doi: 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. doi: 10.1016/j.biocon.2014.12.002

Pe'er, G., Dicks, L. V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T. G., … Scott, A. V. (2014). EU agricultural reform fails on biodiversity. *Science*, *344*(6188), 1090–1092. doi: 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. doi: 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. R Foundation for Statistical Computing, Vienna, Austria. URL 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. doi: 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. doi: 10.1016/j.soilbio.2017.10.016

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., … Tscharntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, *468*(7323), 553–556. doi: 10.1038/nature09492

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*(2), 363–368. doi: 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. doi: 10.1111/j.1365-2486.2008.01557.x

Thompson, P. L., & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, *97*(10), 2867–2879. doi: 10.1002/ecy.1502

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, 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. doi: 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. doi: 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. doi: 10.1016/j.baae.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. doi: 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. doi: 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. doi: 10.1016/j.ecoser.2019.100938

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 hypothetic confidence interval of all possible shapes we can expect for this relationship, respectively.

Figure 2: Sampling biodiversity and ecosystem service supply potential in small forest patches in agricultural landscapes. (A) Sampling locations along the 2500-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 × 5 km^2.

(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.

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 ($p = 0.512$) 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 ($p < 0.05$) 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 ($p = 0.03$) 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 0.33 and 0.48, respectively. The color ramp from red to blue depicts different historical patch ages ranging from the youngest (10 yrs) to the oldest (270 yrs) 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 ($p < 0.05$) 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.

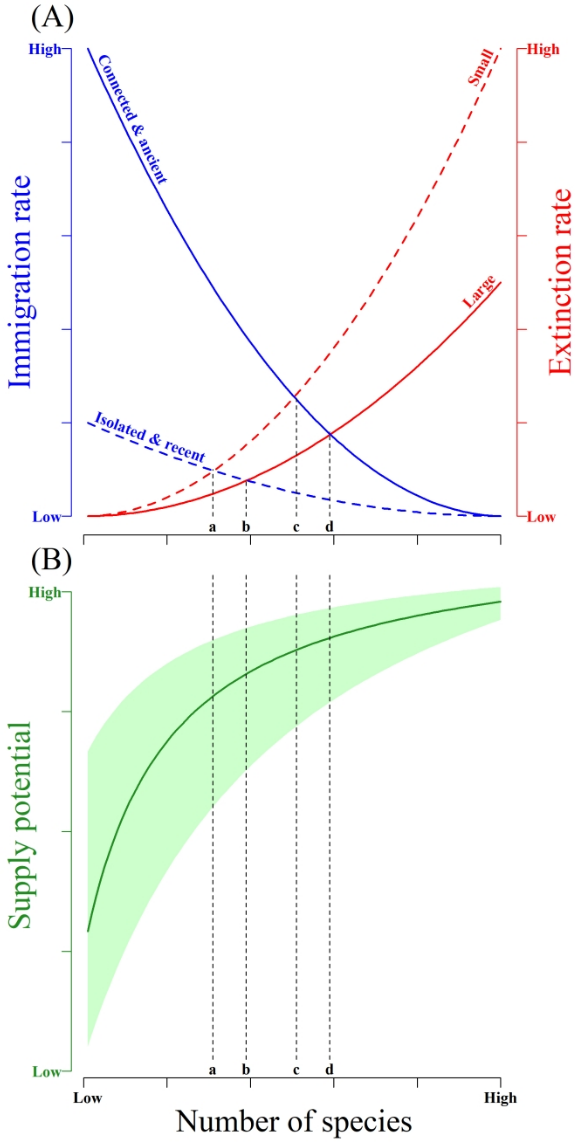


Figure 1: Linking island biogeography (MacArthur & Wilson, 1967) and ecosystem functioning for studying the supply potential of multiple ecosystem services by small forest patches. Hypothetical framework on the effects of forest continuity across space and over time on immigration and extinction rates, 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 hypothetic confidence interval of all possible shapes we can expect for this relationship, respectively.

159x319mm (300 x 300 DPI)

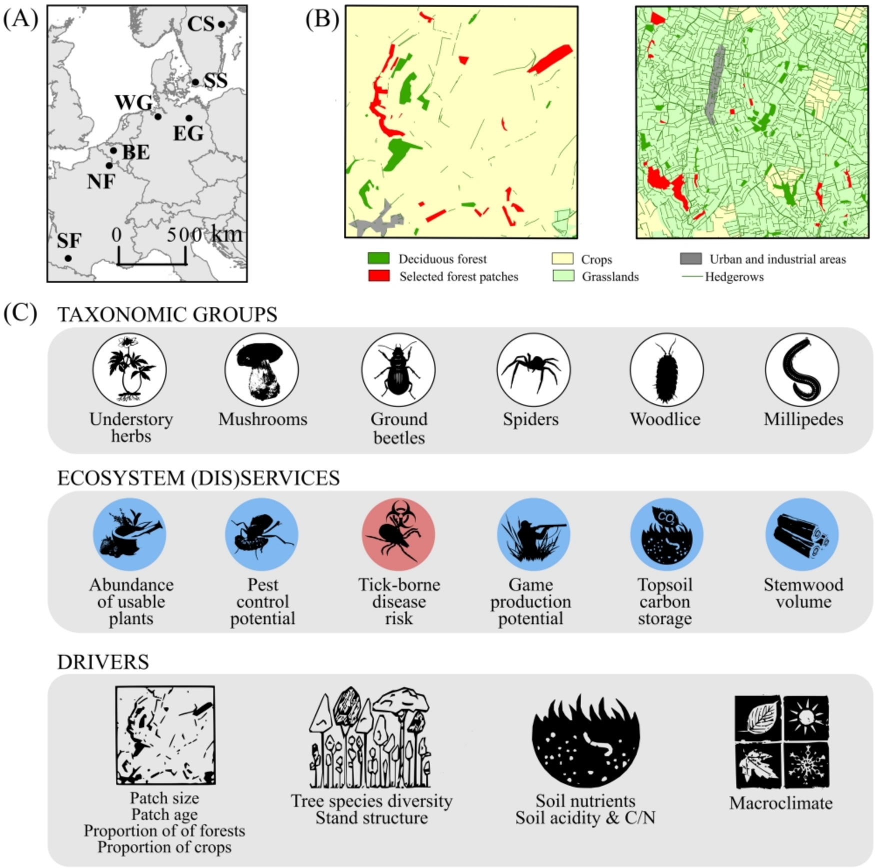


Figure 2: Sampling biodiversity and ecosystem services in small forest patches in agricultural landscapes. (A) Sampling locations along the 2500-km latitudinal gradient in Europe (SF = South France, NF = North France, BE = Belgium, WG = West Germany, EG = East Germany, SS = South Sweden, CS = Central 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 × 5 km2. (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.

245x215mm (300 x 300 DPI)

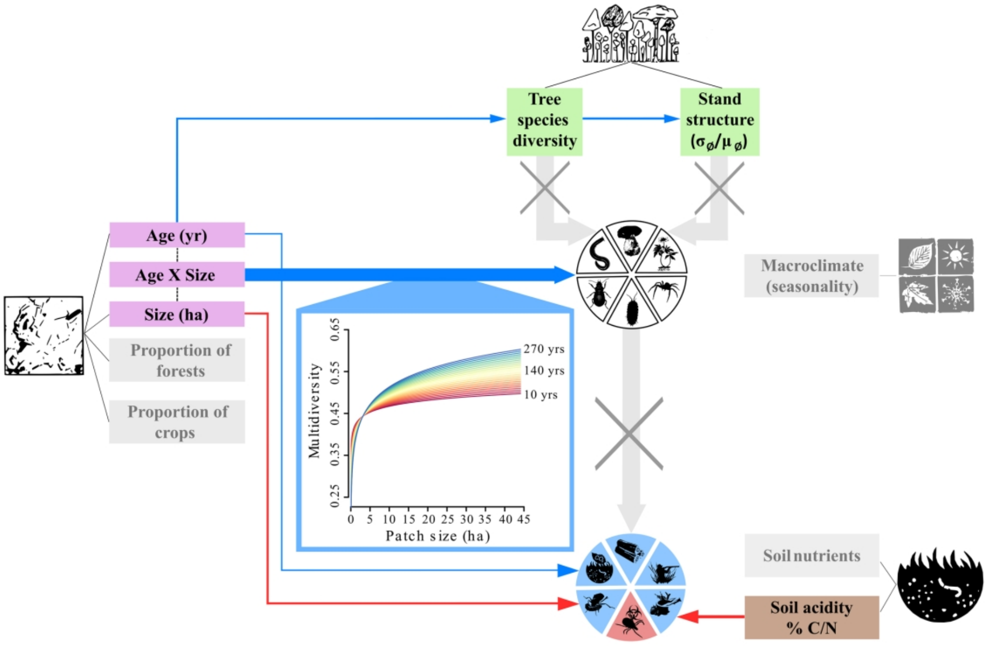
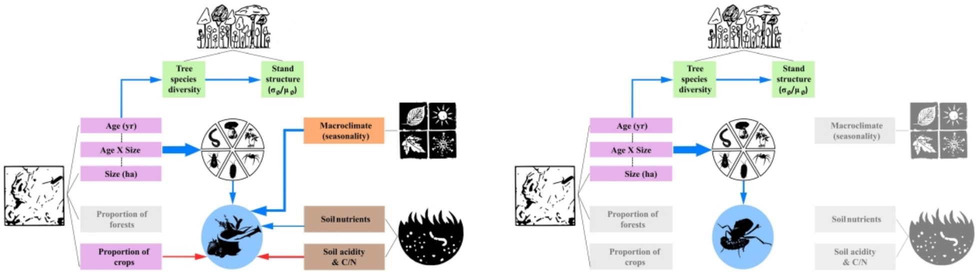


Figure 3: Linkage between the environment, biodiversity and high-performance multiservice delivery in small woodlands across Europe. Results of the piecewise structural equation model (piecewise SEM, p = 0.512) studying the response of high-performance multiservice (MS) delivery to multidiversity, patch 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 ($p < 0.05$) 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 ($p = 0.03$) between patch size and historical age on multidiversity, as predicted by the species-time-area relationship. Marginal (cf. fixed effects) and conditional (fixed and random effects) R2 values are 0.33 and 0.48, respectively. The color ramp from red to blue depicts different historical patch ages ranging from the youngest (10 yrs) to the oldest (270 yrs) 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.

181x119mm (300 x 300 DPI)

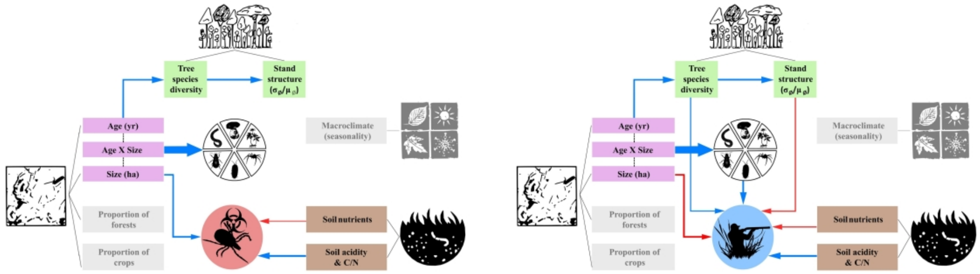
(A) Abundance of usable plants p = 0.524

(B) Pest control potential p = 0.524



(C) Tick-borne disease risk p = 0.396

(D) Game production potential p = 0.370



(E) Topsoil carbon storage p = 0.385

(F) Stemwood volume p = 0.372

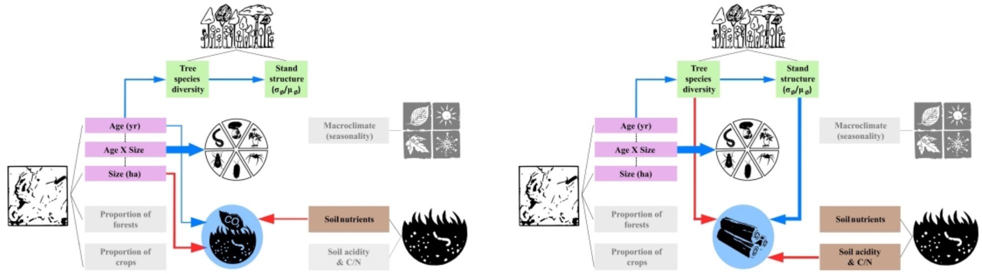


Figure 4: Linkage between the environment, biodiversity and individual ecosystem services in small woodlands across Europe. Results of the piecewise structural equation models studying the response of each individual ecosystem service to multidiversity, patch size, historical age and connectivity (proportion 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 ($p < 0.05$) 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.

294x281mm (300 x 300 DPI)

Supplementary Information

This file contains Appendix S1, Figures S1 to S3 and Tables S1 to S5.

Appendix S1: Supplementary Methods.

Details on patch selection

We wanted the subset of patches selected for sampling to be representative of the variation of patch size and historical age within each window. For that purpose, we divided all patches occurring within a given landscape window into two categories of size (small vs. large patches) and historical age (historically old vs. historically young patches), by using the median values of, respectively, patch size and historical age as division points between categories. Next, we selected 16 patches per window (i.e., 224 patches in total). Our aim was to select four patches for each of the combinations of size times historical age categories (small-old, small-young, large-old, large-young), although due to various reasons (e.g. some patches being unsuitable for sampling) this was not always possible. Summary statistics for each category per landscape window are shown in Table S1).

Details on soil sampling

Soil samples were taken during the period from August to October 2012 before leaves were shed and when the soil was well moisturized. For each patch, we sampled soil evenly along parallel transect lines located 50-m apart from each other. In the smallest patches (less than 7000 m2) a total of 3-5 soil samples were sampled and subsequently pooled. In bigger patches, the number of soil samples were related to patch size, ranging from 5 to 31 soil samples per patch (mean±SE = 5.99±0.26 samples per patch). We used a frame of 25 × 25 cm2 to collect forest floor samples. Care was taken not to mix forest floor with mineral soil when collecting the samples. The mineral soil was sampled using a metal soil core with a diameter of 4.2 cm. One core sample was taken down to 10 cm in mineral soil at all places where forest floor was removed. A total of 1315 forest floor samples and 1315 mineral soil samples were taken.

The samples were dried at 40°C and subsequently weighed. Ten percent of the samples were later dried at 105ºC to establish a correction factor for weight loss. The soil was passed through a 1 mm sieve to remove stones and gravel. Fine and coarse roots were removed by hand and weighed. All samples were analyzed for pH, total carbon (C) and nitrogen (N) as well as total phosphorous (P) in a single laboratory provider. Soil pH (CaCl2) was measured using a glass electrode (Orion, Orion Europe, Cambridge, England, model 920A) following the procedure described in ISO 10390:1994(E). The concentration of C and N was measured by high temperature combustion at 1150°C using an elemental analyzer (Vario MACRO cube CNS, Elementar, Germany). Total P concentration was measured after complete destruction with HClO4 (65%), HNO3 (70%) and H2SO4 (98%) in Teflon bombs for 4 hours at 150°C. P concentrations were measured according to the malachite green procedure (Lajtha, Driscoll, Jarrell, & Elliott, 1999).

For each sample, we calculated the average depth of the forest floor (cm), and the total C and N contents (Mg ha-1), the C:N ratio, the total P content (kg ha-1) and the pH (CaCl2) of the mineral topsoil (0-10 cm).

Details on data collection for forest structural drivers

Data were collected at 1-9 randomly chosen points per patch (number of points depending on patch size, mean±SE = 2.34±0.13) using an adaptation of the Point-Center-Quarter (Cottam & Curtis, 1956) method. Instead of one tree per quarter, two trees per quarter were measured, to gain an increased degree of detail per sample point. Trees were chosen to be of small and large diameter per quadrant and would thus represent different layers/historical age classes of the sampled forest patches. Small trees were chosen to be between 7 cm and 30 cm in diameter at breast height (d130) and larger trees were chosen to be larger than 30 cm at d130. For each tree we recorded the species, tree height, number of stems, d130, the distance and angle to the central sampling point and whether the tree was alive. Sampling was restricted to a 20-m radius around the central point and if no tree of either group was found per quadrant, this was recorded.

Details on data collection for biodiversity

Understory herbs

All patches were comprehensively surveyed for all understory herb (i.e. non-woody) species by walking along parallel transects located 10-m apart from each other. Along these transects, we recorded all species seen and thus obtained a quasi-exhaustive value of understory herb species richness for each patch.

Arthropods

Species richness of arthropods belonging to four taxonomic groups, including ground beetles (Insecta), spiders (Arachnida), millipedes (Myriapoda) and woodlice (Crustacea) was evaluated using pitfall trap sampling. We used pitfall traps with a diameter of 10 cm and a depth of 11 cm. Traps were filled with 200 ml of ethylene glycol and water (1:1). A drop of detergent was added to remove water surface tension and the traps were equipped with aluminum roofs. In order to sample as much of the whole species community a sample point was set-up in the center of each patch and a second one was placed at the south-facing edge of the patch. If the south-facing edge was not suitable e.g. bordered by a ditch, road or other physical barrier (38 % of the edges), we used the eastern (16 % of the edges), western (18 %) or northern edge (4 %) instead. Each sample point consisted of two subsample units spaced five meters from each other. Each subsample unit consisted of two pitfall traps each separated by a plastic barrier (100 cm × 30 cm), parallel to the forest edge. This setup was used originally to identify species fluxes. Thus in each forest patch, eight pitfall traps were set up (four in the core and four at the southern edge). Arthropods were collected twice between April and August 2013. To make data comparable among regions, the two field sampling campaigns started at Growing Degree Hours values of ca. 10,000 and 20,000 (based on data of local weather stations in 2008 and 2009), respectively. Traps were open for 14 consecutive days, after which the trap content was collected and transported to the lab for sorting and subsequent identification. All individuals were identified to the species level.

Mushrooms

In each patch, mushroom species richness was evaluated by recording the presence of all fruiting bodies encountered along a 6-m wide strip-transect disposed along the widest diameter of the patch. Under the general name "mushrooms", we considered only those fungus producing fruiting bodies (i.e. epigeous sporocarps). Mushroom sampling was performed in autumn 2013, and in order to standardize the sampling timing we used six mushroom species with a wide European distribution as phenological indicators: mushroom sampling started as soon as the sporocarps of one of the following taxa were observed: *Armillaria* sp.; *Collybia butyracea*; *C. dryophila*; *Hypholoma fasciculare*; *Laccaria amethystina*; or *Lactarius quietus*. These species frequently occur during the peak of sporocarp production of most species which coincides with a peak in autumn rainfall (Bonet et al., 2008). Local and European encyclopedias and guides (Bon, 2012; Courtecuisse & Duhem, 2013; Eyssartier & Roux, 2013) as well as databases (Société Mycologique du Nord de la France; http://www.smnf.fr/) were used to identify mushroom species in the field. When the species could not be identified in the field, pictures of the whole sporocarps and, when possible, details of the cap, pores, stipe, ring, and gill were taken with a digital camera for species identification.

Details on data collection for proxies for ecosystem services

Abundance of usable plants

We performed a second, more detailed vegetation sampling in each patch, where we walked along parallel transects located 50-m apart from each other and established sampling plots every 100 m along a given transect. Number of sampling plots per patch ranged from 1 (for patches smaller than 0.5 ha) to 128 (mean±SE = 5±0.41). We recorded all vascular species present in the understory within a 10-m radius sampling plot and their abundance in an ordinal scale (1 = rare, 2 = common, 3 = dominant); i.e. a simplified version of the Tansley-scale (Tansley, 1935). We used several bibliographic sources to determine if each of the herbaceous species was of potential use by humans (see usable species list and references in Table S3). We then summed the abundances of usable species for each sampling plot, and calculated the average abundance of usable plants per patch by averaging among all sampling plots within each patch. Note that this variable is completely independent from the variable measuring understory plant diversity, which was obtained from a different survey at a different spatial resolution, i.e. abundance of usable plants was recorded at the plot level whereas understory plant diversity was recorded at the patch level.

Game production potential

Game production potential was assumed to be correlated with the abundance of palatable plants for large herbivores (Gamfeldt et al., 2013) and thus calculated as the average abundance per patch (calculated in a similar way as for usable plants) of the species eaten by roe deer (considering all vascular species, including herbs, shrubs and trees). We checked bibliography on roe deer diet across Europe and selected the vascular plant species (or genus) cited in at least three publications (see species list and references in Table S4). Roe deer was selected since this is an important game species that occurs in all our study regions, which is not the case for, e.g. red deer or wild boar. Roe deer needs woody plant species in its diet (Lovari et al., 2017) and thus requires woodlands or hedgerows within its foraging range. Although there is no direct evidence in the scientific literature to support our hypothesis that roe deer density is positively related to the abundance of palatable plant, we argue that such a positive relationship is very likely and that our approach of using palatable plants as a proxy for game production potential is robust. Indeed, during the hunting season (mostly autumn and winter), when food has become rare for roe deer, both in croplands (harvests are completed and winter wheat has not emerged yet) and grasslands (cattle are still grazing in the meadows at that time of year), roe deer concentrate in woodlands where most of the palatable woody plants for roe deer are still available. Besides, roe deer use woodlands as a shelter against hunters during the hunting season in open farmlands (which starts before the hunting season in woodlands). This increases the probability for roe deer diet to solely rely on woody palatable plants from woodland habitats. Besides, we are not interested in assessing the density of roe deer *per se* here but rather the potential of a given woodland to provide hunting recreational activities and thus game production potential should be seen here as a recreational service rather than as a pure provisioning service for food supply.

Pest control potential

Pest control potential was assessed by the total abundance of malacophagous carabid beetles per patch from trapping data (see above and Table S5 for the list of malacophagous species and references). The rationale is that the selected malacophagous carabid beetles will prey on slugs in the adjacent fields; i.e. they use the forest patches for overwintering and refuge against agricultural disturbances and migrate to the agricultural land to prey (see references in Table S5). Note that abundance values from a very restricted set of species (malacophagous beetles) were used here to compute pest control potential whereas the variable measuring arthropod diversity is based on occurrence data across four different arthropod groups.

Tick-borne disease risk

Tick-borne disease risk (a disservice) was assumed to be correlated with tick density because a higher tick density would result in a higher risk for humans to be infected by tick-borne diseases such as Lyme Borreliosis. For each patch, tick density (i.e. mean density of nymphs per 100 m^2) was assessed using a standardized sampling protocol. All ticks stages were collected via drag sampling (Tack et al., 2011) with a 1 × 1 m^2 piece of white flannel fabric attached to a wooden pole on a 100-m long transect (resulting in a 100 m^2 sampled area). Ticks were collected in the close vicinity (less than 25 m distance) of the central sampling point used for forest structure (see above). Ticks were picked off the cloth after 25 m of dragging and preserved in ethanol before being identified at the species level and counted in the lab (Ehrmann et al., 2017).

Stemwood volume

Stemwood volume (m^3) was determined from published species- and region-specific allometric equations based on tree height and diameter at breast height (d130) measurements. Species-specific equations to calculate stemwood volume are not available for all regions, and some species found in forests are not represented by any equation in the literature. Thus, either generalized regional equations (regional *Quercus* equation for all *Quercus* trees in that region, irrespective of species), generalized equations irrespective of the region, equations from substitute species (*Quercus robur* for *Castanea sativa*) or generic equations based merely on d130 and tree height, if no equations were available for the respective species (Deleuze et al., 2014), were used in order to calculate stemwood volume (see https://github.com/EhrmannS/tree-allometry for a detailed description of the selection of utilized equations).

Topsoil carbon storage

We used the soil C content (Mg/ha) in the combined forest floor and mineral topsoil (10 cm) for each patch as a measure of the potential for topsoil carbon storage.

REFERENCES

Bon, M. (2012). Champignons de France et d'Europe. Flammarion.

Bonet, J. A., Pukkala, T., Fischer, C. R., Palahí, M., De Aragón, J. M., & Colinas, C. (2008). Empirical models for predicting the production of wild mushrooms in Scots pine (*Pinus sylvestris* L.) forests in the Central Pyrenees. Annals of Forest Science, 65(2), 206–206.

Cottam, G., & Curtis, J. T. (1956). The use of distance measures in phytosociological sampling. Ecology, 37(3), 451. Doi:10.2307/1930167

Courtecuisse, R., & Duhem, B. (2013). Champignons de France et d'Europe. Paris : Delachaux et Niestlé.

Deleuze, C., Morneau, F., Renaud, J. P., Vivien, Y., Rivoire, M., Santenoise, P., … Vallet, P. (2014). Estimer le volume total d'un arbre, quelles que soient l'essence, la taille, la sylviculture, la station. *Rendez-Vous Techniques ONF*, (44), 22–32.

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, 31. Doi:10.1186/s12898-017-0141-0

Eyssartier, G., & Roux, P. (2013). Le Guide des champignons – France et Europe (3^e édition). Paris: Belin literature et revues.

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. Doi:10.1038/ncomms2328

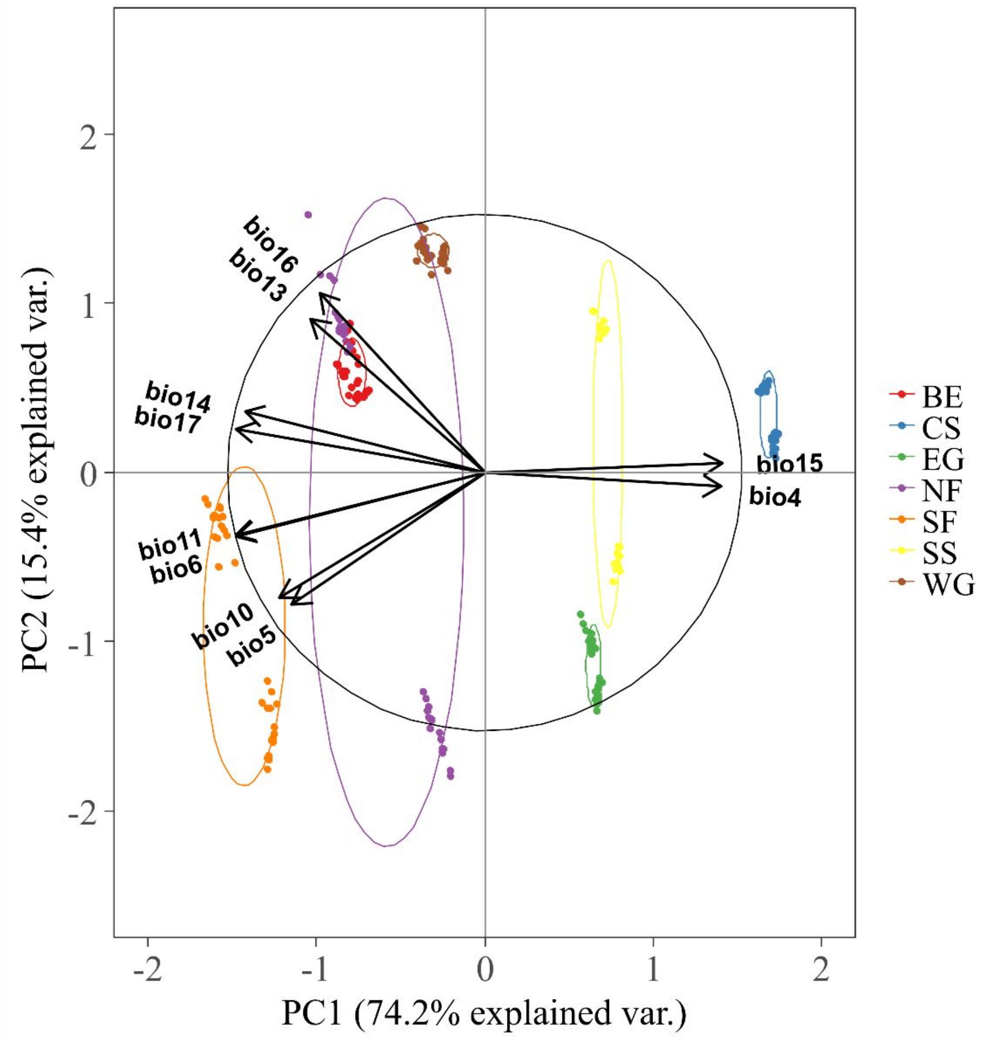
Lajtha, K., Driscoll, C. T., Jarrell, W. M., & Elliott, E. T. (1999). Soil phosphorus: characterization and total element analysis. In Standard soil methods for long-term ecological research. New York: Oxford University Press. P (pp. 115–42).

Lovari, S., Serrao, G., & Mori, E. (2017). Woodland features determining home range size of roe deer. *Behavioural Processes*, 140, 115–120.

Tack, W., Madder, M., Frenne, P. D., Vanhellemont, M., Gruwez, R., & Verheyen, K. (2011). The effects of sampling method and vegetation type on the estimated abundance of *Ixodes ricinus* ticks in forests. Experimental and Applied Acarology, 54(3), 285–292. Doi:10.1007/s10493-011-9444-6

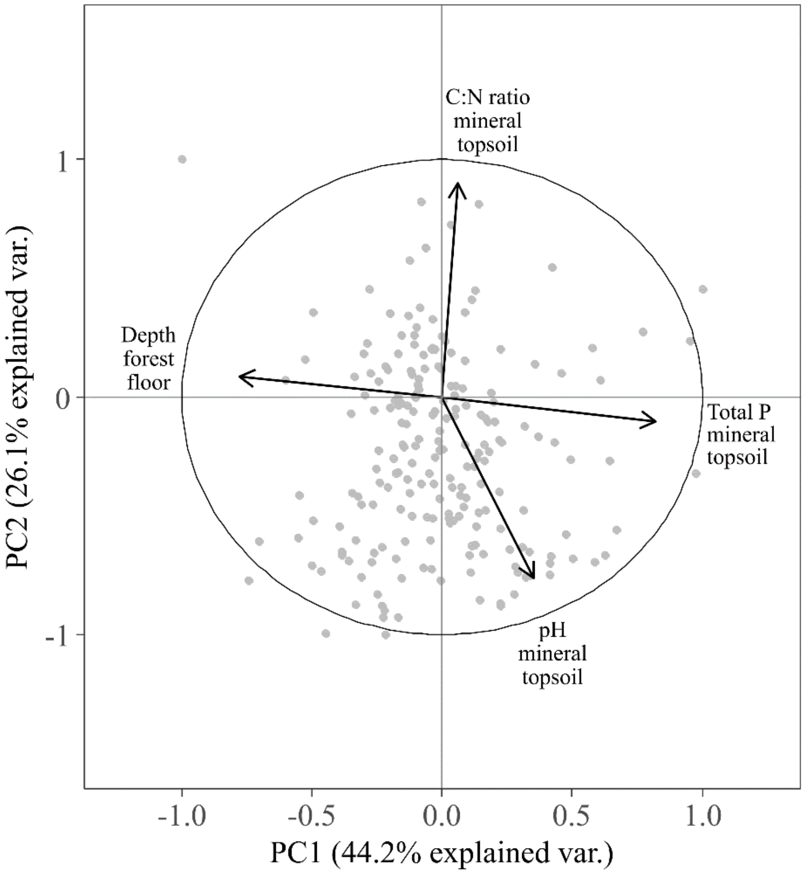
Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, *16*(3), 284–307.

Figure S1: Diagram of the principal component analysis (PCA) used to calculate the variable "macroclimate". The PCA included 5 temperature variables (BIO4 = temperature seasonality, BIO5 = maximum temperature of warmest month, BIO6 = minimum temperature of coldest month, BIO10 = mean temperature of warmest quarter, BIO11 = mean temperature of coldest quarter) and 5 precipitation variables (BIO15 = precipitation seasonality, BIO13 = precipitation of wettest month, BIO14 = precipitation of driest month, BIO16 = precipitation of wettest quarter, BIO17 = precipitation of driest quarter). The correlation of each variable with the two first PCA axes is shown. The black circle represents correlation = 1. Points correspond to observations (patches) classified by region (SF = South France, NF = North France, BE = Belgium, WG = West Germany, EG = East Germany, SS = South Sweden, CS = Central Sweden). Colored ellipses include 68% of the patches in each region.


bio16
bio13
bio14
bio17
bio11
bio6
bio10
bio5
bio15
bio4
2
1
0
-1
-2
PC2 (15.4% explained var.)
-2
-1
0
1
2
PC1 (74.2% explained var.)
BE
CS
EG
NF
SF
SS
WG

232

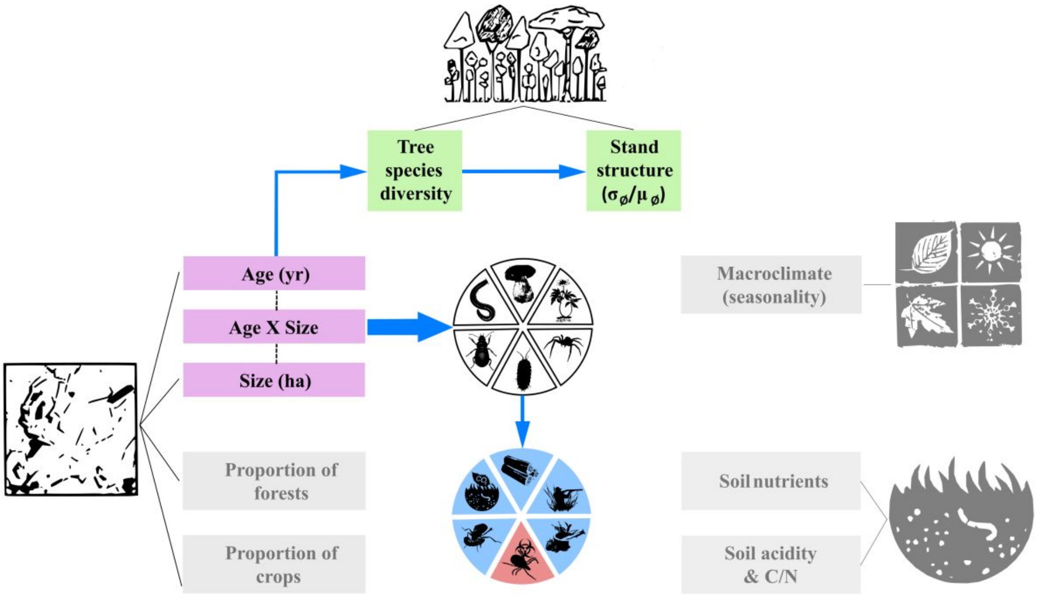
Figure S2: Diagram of the principal component analysis (PCA) used to calculate the variables “soil nutrients” (PCA axis 1) and “soil acidity & C/N” (PCA axis 2). The PCA included 4 variables: depth of the forest floor and C:N ratio, total P content and pH of the mineral topsoil. The correlation of each variable with the



two first PCA axes is shown. The black circle represents correlation = 1. Points correspond to observations (patches).

Figure S3: Linkage between the environment, biodiversity and multiservice delivery potential in small woodlands across Europe. Results of the piecewise structural equation models (piecewise SEMs) studying the response of low- (A) and intermediate-performance (B) multiservice (MS) 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. The variables "region" and "window type" nested within "region" were included as random effect terms in all component models. Blue arrows indicate positive effects and red arrows indicate negative effects. Arrow thickness is proportional to the effect size. Only significant effects ($p < 0.05$) are shown, while variables not significantly contributing to the models are attenuated and represented with grey shading. According to Fisher's C statistic, both SEMs provided an adequate fit to the data with all p-values all above the 0.05 threshold. The p-value for the global model is shown in each case.

(A) Low-performance MS delivery potential p = 0.477



(B) Intermediate-performance MS delivery potential p = 0.373

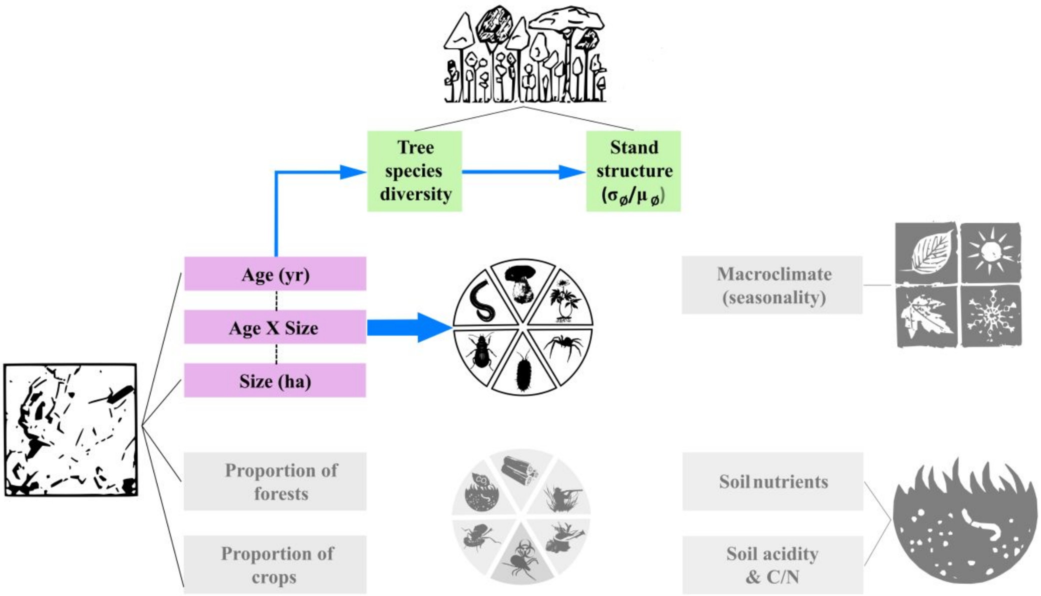


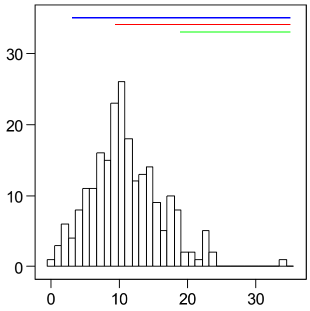
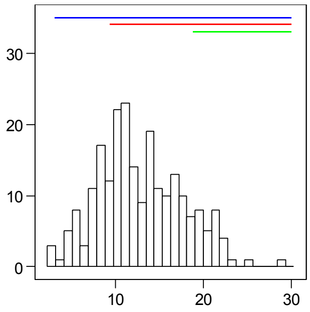
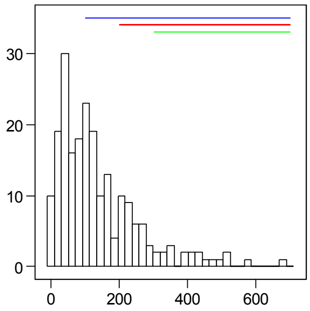
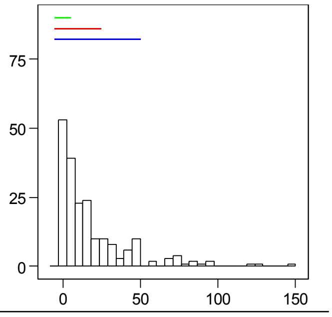
Table S1: Summary statistics for each patch size and age category per landscape window. Means and standard deviations (SD) of size and age of the patches are shown, as well as the number of patches included in each category (N).

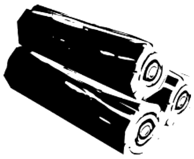
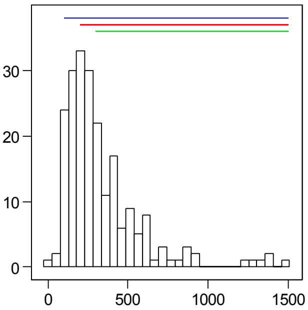
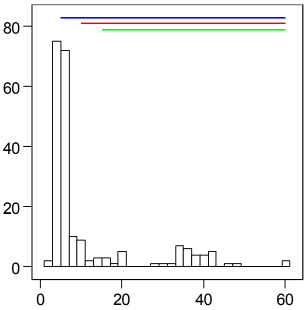
Landscape window	**Size category**	**Age category**	**N**	**Size (ha)**		**Age (years)**	
				Mean	**SD**	**Mean**	**SD**
Be_B	large	old	4	11.19	4.46	131.88	22.9
	large	recent	4	2.45	1.58	20.79	15.11
	small	old	4	0.61	0.27	110.45	21.15
	small	recent	4	0.82	0.5	21.04	18.07
Be_O	large	old	4	9.21	2.77	210.25	12.4
	large	recent	4	2.25	1.65	51.33	45.96
	small	old	4	0.58	0.4	212.73	33.67
	small	recent	4	0.44	0.16	54.26	48.9
Fr_N_B	large	old	4	9.54	12.04	79.36	42.32
	large	recent	4	1.59	0.54	24.6	9.04
	small	old	4	0.59	0.26	50.84	8.75
	small	recent	4	0.38	0.28	12	0
Fr_N_O	large	old	4	12.62	10.3	133.47	20.66
	large	recent	4	3.06	1.02	43.82	21.32
	small	old	4	1.28	0.65	90.76	19.48
	small	recent	4	0.66	0.58	39.02	18.83
Fr_S_B	large	old	4	4.05	2.35	91.91	34.87
	large	recent	4	4.88	3.07	31.69	16.34
	small	old	4	0.53	0.21	44.74	4.59

	small	recent	4	0.41	0.17	17.16	10.32
Fr_S_O	large	old	5	9.04	2.99	125.44	6.4
	large	recent	3	4.27	1.66	12	0
	small	old	4	1.18	0.48	88.86	50.69
	small	recent	4	0.55	0.18	12	0
Ge_E_B	large	old	8	5.8	3.42	122.27	69
	large	recent	0	-	-	-	-
	small	old	1	2.48	-	70.51	-
	small	recent	7	1.14	0.39	12	0
Ge_E_O	large	old	7	21.4	17.71	136.03	38.75
	large	recent	2	2.87	1.03	57.65	48.49
	small	old	2	2.05	0.4	119.32	41.59
	small	recent	7	0.89	0.35	21.82	25.97
Ge_W_B	large	old	4	7.2	5.14	107.17	50.09
	large	recent	4	2.34	0.57	12	0
	small	old	4	0.72	0.44	115.08	90.8
	small	recent	4	0.37	0.13	12	0
Ge_W_O	large	old	4	7.2	6.53	139.73	39.46
	large	recent	1	1.82	-	37.29	-
	small	old	4	0.82	0.36	101.21	42.35
	small	recent	7	0.73	0.47	22.31	14.34
Sw_C_B	large	old	4	0.94	0.7	90.91	76.82
	large	recent	4	1.08	0.26	13.11	2.21
	small	old	4	0.28	0.06	87.53	43.11
	small	recent	4	0.18	0.1	12	0

Sw_C_O	large	old	4	2.74	1.84	125.85	95.19
	large	recent	4	4.78	5.79	12	0
	small	old	4	0.62	0.2	48.09	14.82
	small	recent	4	0.64	0.19	17.08	10.17
Sw_S_B	large	old	10	9.48	10.32	202.9	53
	large	recent	2	2.14	0	57.98	65.02
	small	old	1	0.38	-	107.6	-
	small	recent	3	0.86	0.33	35.04	18.31
Sw_S_O	large	old	7	8.85	8.08	90.5	45.22
	large	recent	2	7.01	6.47	24.46	17.62
	small	old	1	2.2	-	235.42	-
	small	recent	6	1.08	0.46	23.59	18.19

Table S2: Details on the definition of thresholds of low, intermediate and high performance levels of multiservice delivery for each individual ecosystem service proxy. The blue, red, and green lines above the histograms entail patches with low, intermediate, and high performance levels, respectively. Abundances of usable plants and game production potential were calculated as averages of abundances among all sampling plots within each patch. Each sampling plot was a circle of 10-m radius (314 m^2) where abundances of individual species were recorded in an ordinal scale (1 = rare, 2 = common, 3 = dominant; i.e. a simplified version of the Tansley-scale (Tansley, 1935)) and summed. For these two ecosystem services we have chosen threshold values that represent different abundances per 100 m^2. In general, the threshold values aimed to reflect tangible values that are meaningful for practitioners, and were determined after consultation of the literature for pest control potential (Rouabah, Villerd, Amiaud, Plantureux, & Lasserre-Joulin, 2015), tick-borne disease risk (Ruyts et al., 2018), stemwood volume (FAO, 2015a, 2015b) and topsoil carbon storage (Vesterdal, Schmidt, Callesen, Nilsson, & Gundersen, 2008). The thresholds for the abundance of usable plants and the game production potential were based on expert judgment by the paper's core author team (AV, JL, PDF, KV, and GD) since literature data were lacking.

Ecosystem service proxy	Units	Threshold values			Histogram
		Low	Medium	High	
 Abundance of usable plants	Mean total cover in a 10 m radius plot (314 m²). Cover scale: 1 rare; 2 common; 3 dominant. Usable plants are defined in Table S3. The more abundant they are, the higher the production	> 1 rare species per 100 m² (i.e. value of 3.14)	> 1 dominant species per 100 m² (i.e. 9.42)	> 2 dominant species per 100 m² (i.e. 18.84)	
 Game production potential	For the game production potential we assumed that a high abundance of plants palatable for roe deer (see Table S4) is positively linked to the abundance of roe deer; an important game species in the studied landscapes	> 1 rare species per 100 m² (i.e. value of 3.14)	> 1 dominant species per 100 m² (i.e. 9.42)	> 2 dominant species per 100 m² (i.e. 18.84)	
 Pest control potential	Number of slug-eating carabids found in 8 pitfall traps during two trapping periods. We assume that a high carabid abundance will decrease slug abundance (thus increasing the pest control potential)	> 100	> 200	> 300	
 Tick-borne disease risk	Mean nymphs density per 100 m². Density of nymphs determines the density of Borrelia- infected nymphs, which is a key proxy for disease risk	< 50	< 25	< 5	

 Stemwood volume	Total stemwood volume (m³/ha). This volume determines the potential for wood production in a forest patch	> 100	> 200	> 300	
 Topsoil carbon storage	Forest floor + topsoil (0-10 cm) (Mg/ha). We assume that higher topsoil stocks are the result of higher carbon sequestration rates	> 5	> 10	> 15	

REFERENCES

Food and Agriculture Organization of the United States (FAO) (2015a). Global Forest Resources Assessment 2015: How are the world's forests changing? Retrieved from http://www.fao.org/forest-resources-assessment/en/

Food and Agriculture Organization of the United States (FAO) (2015b). Global Forest Resources Assessment 2015. Desk reference. Retrieved from http://www.fao.org/forest-resources-assessment/en/

Rouabah, A., Villerd, J., Amiaud, B., Plantureux, S., & Lasserre-Joulin, F. (2015). Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. *Agriculture, Ecosystems & Environment*, *200*, 21–32. doi: 10.1016/j.agee.2014.10.011

Ruyts, S. C., Tack, W., Ampoorter, E., Coipan, E. C., Matthysen, E., Heylen, D., … Verheyen, K. (2018). Year-to-year variation in the density of Ixodes ricinus ticks and the prevalence of the rodent-associated human pathogens Borrelia afzelii and B. miyamotoi in different forest types. *Ticks and Tick-Borne Diseases*, *9*(2), 141–145.

Tansley, A. G. (1935). The use and abuse of vegetational concepts and terms. *Ecology*, *16*(3), 284–307.

Vesterdal, L., Schmidt, I. K., Callesen, I., Nilsson, L. O., & Gundersen, P. (2008). Carbon and nitrogen in forest floor and mineral soil under six common European tree species. *Forest Ecology and Management*, *255*(1), 35–48. doi: 10.1016/j.foreco.2007.08.015

Table S3: List of understory forest herb species present in the sampled forest patches and considered to be of potential use for humans. We used several bibliographic sources (Couplan, 2009; Ducerf, 2013; Mabey & Blamey, 1989; Mears & Hillman, 2007; Tobyn, Denham, & Whitelegg, 2016) to determine if each of the understory herb species found in the vegetation surveys was of potential use by humans. We used Couplan (2009) as the primary source, as it was the most complete, providing detailed indications on plant uses. Uses were divided in 3 categories: food use, medicinal use and other uses. Plant use was only considered when used in Europe (from France to Scandinavia, from the United Kingdom to Poland). Supposed or potential uses were not considered and only realized uses were considered. Plants that are used but which are not forest or forest edge species have not been considered, as forest populations of these species will never be used because there are much larger populations outside forests (e.g. *Papaver rhoeas*, *Hypochoeris radicata*, *Chenopodium album*, *Lamium album*, *Plantago* spp., etc.).

Species name	Food	Medicinal	Other
Adoxa moschatellina	X	X	
Aegopodium podagraria	X	X	
Agrimonia eupatoria	X	X	X
Ajuga reptans	X	X	
Alliaria petiolata	X	X	
Allium oleraceum	X		
Allium schoenoprasum	X		
Allium scorodoprasum	X		
Allium ursinum	X		
Allium vineale	X		
Anacamptis morio	X	X	
Anacamptis pyramidalis	X		
Angelica sylvestris	X	X	
Anthemis tinctoria		X	
Anthoxanthum odoratum	X	X	
Anthriscus caucalis	X		
Anthriscus sylvestris	X		
Aquilegia vulgaris	X		X
Arctium lappa	X	X	

Arctium minus	X	X	
Arctium tomentosum	X	X	
Arrhenatherum elatius ssp. bulbosum	X		
Arum italicum	X	X	
Arum maculatum	X	X	
Arum sp.	X	X	
Asphodelus albus	X		X
Asplenium trichomanes		X	
Bryonia dioica	X	X	
Calla palustris	X		
Campanula trachelium	X		
Cardamine amara	X		
Cardamine flexuosa	X		
Cardamine impatiens	X		
Cardamine pratensis	X	X	
Centaurium erythraea	X		
Cerastium semidecandrum	X		
Chrysosplenium alternifolium	X		
Chrysosplenium oppositifolium	X		
Cirsium oleraceum	X		
Cirsium palustre	X		
Cistus salviifolius	X		
Clinopodium sp.		X	
Clinopodium vulgare (Satureja vulgaris)	X		
Conopodium majus	X		
Dactylis glomerata	X		
Dactylorhiza maculata	X		
Deschampsia cespitosa	X		
Deschampsia flexuosa (Avenella flexuosa)	X		
Dipsacus fullonum	X		
Dryopteris filix-mas	X	X	
Elytrigia repens (Elymus repens)	X	X	
Epilobium angustifolium	X		
Epilobium montanum	X	X	
Epilobium palustre	X		
Epilobium parviflorum	X	X	
Epilobium tetragonum	X		
Equisetum arvense	X	X	X
Equisetum fluviatile	X	X	X
Equisetum hyemale	X	X	X
Equisetum palustre	X	X	X
Equisetum pratense		X	X
Equisetum ramosissimum		X	X
Equisetum sp.		X	X
Equisetum sylvaticum	X	X	X
Equisetum telmateia	X	X	X

Euphorbia amygdaloides			X
Euphorbia dulcis			X
Euphorbia cyparissias			X
Filipendula ulmaria	X	X	X
Fragaria moschata	X		
Fragaria vesca	X	X	
Galanthus nivalis	X		X
Galeopsis bifida_tetrahit	X		
Galium aparine	X		
Galium odoratum (Asperula odorata)	X	X	X
Galium verum	X		X
Genista tinctoria	X	X	X
Geum rivale	X	X	
Geum urbanum	X	X	
Glechoma hederacea	X	X	
Glyceria fluitans	X		
Heracleum sphondylium	X	X	
Humulus lupulus	X	X	X
Hyacinthoides non-scripta			X
Hypericum perforatum	X	X	X
Hypericum tetrapterum (Hypericum quadrangulum)	X		
Lamium galeobdolon (Galeobdolon luteum)	X		
Lamium maculatum	X		
Lapsana communis	X	X	
Lathyrus linifolius	X		
Lathyrus linifolius var. montanus	X		
Lathyrus sylvestris	X		
Leucojum vernum			X
Lunaria rediviva			X
Lythrum portula (Peplis portula)	X	X	
Lythrum salicaria	X		
Maianthemum bifolium	X		
Mentha aquatica	X		
Milium effusum	X		
Moehringia trinervia	X		
Monotropa hypopitys	X	X	
Mycelis muralis (Lactuca muralis)	X		
Nasturtium officinale	X	X	
Orchis mascula	X	X	
Orchis purpurea	X	X	
Origanum vulgare	X	X	
Ornithogalum pyrenaicum	X		
Ornithogalum umbellatum	X		X
Oxalis acetosella	X	X	
Phyteuma nigrum	X		
Phyteuma spicatum	X		

Picris echioides	X		
Picris hieracioides	X		
Platanthera bifolia	X	X	
Polygonatum multiflorum	X		
Polygonatum odoratum	X	X	
Polygonum amphibium	X		
Polygonum bistorta	X		
Polypodium vulgare	X		
Potentilla erecta		X	
Primula elatior	X	X	
Primula veris	X	X	
Primula vulgaris	X	X	
Prunella vulgaris	X	X	
Pteridium aquilinum	X		X
Pulmonaria obscura	X		
Pulmonaria officinalis	X	X	
Rubia peregrina	X		X
Rumex obtusifolius	X	X	
Rumex sanguineus	X	X	
Ruscus aculeatus	X	X	X
Sambucus ebulus			X
Sanicula europaea		X	
Scirpus sylvaticus	X		
Scrophularia nodosa		X	
Sedum telephium	X		X
Sedum telephium subsp. maximum	X		X
Senecio viscosus		X	
Silene vulgaris	X		X
Solanum dulcamara			X
Solanum nigrum			X
Solidago virgaurea		X	
Spartium junceum		X	
Stachys officinalis		X	
Stachys sylvatica	X	X	
Stellaria alsine (Stellaria uliginosa)	X		
Stellaria media	X	X	
Stellaria nemorum	X	X	
Succisa pratensis		X	
Symphytum officinale	X	X	
Tamus communis	X	X	
Teucrium scorodonia		X	
Thymus serpyllum	X		
Typha angustifolia	X	X	
Typha latifolia	X	X	
Urtica dioica	X	X	X
Vaccinium myrtillus	X	X	

Vaccinium uliginosum	X	X	
Vaccinium vitis-idaea	X	X	
Valeriana officinalis (Valeriana repens)	X	X	
Veronica officinalis	X	X	
Vicia sepium	X		
Viola odorata	X		X
Viola reichenbachiana	X		X
Viola riviniana	X		

REFERENCES

Couplan, F. (2009). *Le régal végétal: plantes sauvages comestibles* (Vol. 1). Editions Ellebore.

Ducerf, G. (2013). *L'encyclopédie des plantes bio-indicatrices alimentaires et médicinales: guide de diagnostic des sols*. Promonature.

Mabey, R., & Blamey, M. (1989). *Food for free*. Collins.

Mears, R., & Hillman, G. C. (2007). *Wild food*. Hodder & Stoughton.

Tobyn, G., Denham, A., & Whitelegg, M. (2016). *The Western herbal tradition: 2000 years of medicinal plant knowledge*. Singing Dragon.

Table S4: List of species present in the sampled forest patches and considered to be palatable for roe deer, i.e. cited in at least three of the references consulted hereafter: Barančeková, 2004; Barančeková, Krojerová-Prokešová, Šustr, & Heurich, 2010; Bartolomé, Rosell, & Bassols, 2002; Cederlund & Nyström, 1981; Czernik et al., 2013; de Jong, Gill, van Wieren, & Burlton, 1995; Helle, 1980; Henry, 1975; Jackson, 1980; Kamler & Homolka, 2005; Maizeret, Boutin, Cibien, & Carlino, 1989; Moser, Schütz, & Hindenlang, 2008; Mysterud, Lian, & Hjermann, 1999; Schmidt, Sommer, Kriebitzsch, Ellenberg, & Oheimb, 2004; Storms et al., 2008; Tixier et al., 1997; and Wallach, Shanas, & Inbar, 2010.

Species name
Agrostis canina
Agrostis capillaris (Agrostis tenuis)
Agrostis gigantea
Agrostis sp.
Agrostis stolonifera
Betula pendula
Betula pubescens
Calluna vulgaris
Carex acuta
Carex acutiformis
Carex appropinquata
Carex brunnescens
Carex buxbaumii
Carex canescens (Carex curta)
Carex cespitosa
Carex cuprina
Carex demissa (Carex viridula subsp. oedocarpa)
Carex diandra
Carex digitata
Carex divulsa
Carex echinata
Carex elata
Carex elongata
Carex flacca
Carex flava
Carex hirsuta
Carex hirta
Carex loliacea
Carex montana

Carex muricata agg.
Carex nigra
Carex ovalis (Carex leporina)
Carex pallescens
Carex pendula
Carex pilulifera
Carex pseudobrizoides
Carex pseudocyperus
Carex remota
Carex riparia
Carex rostrata
Carex sp.
Carex spicata agg.
Carex strigosa
Carex sylvatica
Carex umbrosa
Carex vaginata
Carex vesicaria
Carex vulpina
Deschampsia cespitosa
Deschampsia flexuosa (Avenella flexuosa)
Fagus sylvatica
Festuca arundinacea
Festuca gigantea
Festuca heterophylla
Festuca ovina agg.
Festuca pratensis
Festuca rubra
Festuca sp.
Hedera helix
Holcus lanatus
Holcus mollis
Luzula campestris
Luzula forsteri
Luzula luzuloides
Luzula multiflora
Luzula pallescens
Luzula pilosa
Luzula sp.
Picea abies
Picea sitchensis
Pinus sylvestris
Poa annua
Poa bulbosa
Poa nemoralis
Poa palustris

Poa pratensis
Poa pratensis ssp. *angustifolia (Poa angustifolia)*
Poa sp.
Poa trivialis
Populus tremula
Prunus avium
Prunus cerasifera
Prunus cerasifera f. *atropurpurea*
Prunus cerasus
Prunus domestica ssp. *insititia*
Prunus laurocerasus
Prunus mahaleb
Prunus padus (Padus avium)
Prunus serotina
Prunus sp.
Prunus spinosa
Quercus ilex
Quercus petraea
Quercus pubescens
Quercus robur
Quercus rubra
Quercus sp.
Rubus caesius
Rubus fruticosus agg.
Rubus idaeus
Rubus saxatilis
Rubus sp.
Rubus spectabilis
Rumex acetosa
Rumex acetosella
Rumex conglomeratus
Rumex crispus
Rumex longifolius
Rumex obtusifolius
Rumex sanguineus
Rumex sp.
Salix alba
Salix aurita
Salix caprea
Salix cinerea
Salix fragilis
Salix pentandra
Salix sp.
Salix triandra
Salix viminalis
Sorbus aucuparia

Urtica dioica
Vaccinium myrtillus
Vaccinium vitis-idaea

REFERENCES

Barančeková, M. (2004). The roe deer diet: is floodplain forest optimal habitat? *Folia Zool*, *53*(3), 285–292.

Barančeková, M., Krojerová-Prokešová, J., Šustr, P., & Heurich, M. (2010). Annual changes in roe deer (*Capreolus capreolus* L.) diet in the Bohemian Forest, Czech Republic/Germany. *European Journal of Wildlife Research*, *56*(3), 327–333. doi:10.1007/s10344-009-0321-0

Bartolomé, J., Rosell, C., & Bassols, E. (2002). Diet composition of roe deer (*Capreolus capreolus*) in the Natural Park of the Garrotxa volcanic zone (Catalonia, Spain). *Pirineos*, *157*(0), 57–64. doi:10.3989/pirineos.2002.v157.61

Cederlund, G., & Nyström, A. (1981). Seasonal differences between moose and roe deer in ability to digest browse. *Holarctic Ecology*, *4*(1), 59–65.

Czernik, M., Taberlet, P., Świs\locka, M., Czajkowska, M., Duda, N., & Ratkiewicz, M. (2013). Fast and efficient DNA-based method for winter diet analysis from stools of three cervids: moose, red deer, and roe deer. *Acta Theriol*, *58*, 379–386.

de Jong, C. B., Gill, R. M. A., van Wieren, S. E., & Burlton, F. W. E. (1995). Diet selection by roe deer *Capreolus capreolus* in Kielder Forest in relation to plant cover. *Forest Ecology and Management*, *79*(1–2), 91–97. doi:10.1016/0378-1127(95)03622-9

Helle, P. (1980). Food composition and feeding habits of the roe deer in winter in central Finland. *Acta Theriologica*, *25*(32), 395–402.

Henry, B. A. M. (1975). *Dispersion, diet and criteria of age of roe deer (*Capreolus capreolus *L.) in Hamsterley forest, county Durham* (Doctoral). Durham University. Retrieved from http://etheses.dur.ac.uk/8178/

Jackson, J. (1980). The annual diet of the roe deer (*Capreolus capreolus*) in the New Forest, Hampshire, as determined by rumen content analysis. *Journal of Zoology*, *192*(1), 71–83. doi:10.1111/j.1469-7998.1980.tb04220.x

Kamler, J., & Homolka, M. (2005). Faecal nitrogen: a potential indicator of red and roe deer diet quality in forest habitats. *Folia Zoologica Praha*, *54*(1/2), 89.

Maizeret, C., Boutin, J.-M., Cibien, C., & Carlino, J.-P. (1989). Effects of population density on the diet of roe deer and the availability of their food in Chizé forest. *Acta Theriol*, *34*, 235–246.

Moser, B., Schütz, M., & Hindenlang, K. E. (2008). Resource selection by roe deer: Are windthrow gaps attractive feeding places? *Forest Ecology and Management*, *255*(3–4), 1179–1185. doi:10.1016/j.foreco.2007.10.023

Mysterud, A., Lian, L.-B., & Hjermann, D. Ø. (1999). Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. *Canadian Journal of Zoology*, *77*, 1486–1493.

Schmidt, M., Sommer, K., Kriebitzsch, W.-U., Ellenberg, H., & Oheimb, G. von. (2004). Dispersal of vascular plants by game in northern Germany. Part I: Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). *European Journal of Forest Research*, *123*(2), 167–176. doi:10.1007/s10342-004-0029-3

Storms, D., Aubry, P., Hamann, J.-L., Saïd, S., Fritz, H., Saint-Andrieux, C., & Klein, F. (2008). Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildlife Biology*, *14*(2), 237–250. doi:10.2981/0909-6396(2008)14[237:SVIDCA]2.0.CO;2

Tixier, H., Duncan, P., Scehovic, J., Yant, A., Gleizes, M., & Lila, M. (1997). Food selection by European roe deer (*Capreolus capreolus*): effects of plant chemistry, and consequences for the nutritional value of their diets. *Journal of Zoology*, *242*(2), 229–245. doi:10.1111/j.1469-7998.1997.tb05799.x

Wallach, A. D., Shanas, U., & Inbar, M. (2010). Feeding activity and dietary composition of roe deer at the southern edge of their range. *European Journal of Wildlife Research*, *56*(1), 1–9. doi:10.1007/s10344-009-0281-4

Table S5: List of carabid species present in the sampled forest patches considered as malacophagous according to the references consulted hereafter: Bohan et al., 2000; Brandmayr & Brandmayr, 1986; Cornic, 1973; Dajoz, 2002; Davies, 1953; Dennison & Hodkinson, 1983; Fawki & Toft, 2005; Grimm, Paill, & Kaiser, 2000; Gruntal & Sergeyeva, 1989; Henderson et al., 1996; Holland, 2002; Jelaska, Franjevic, JelASKA, & Symondso, 2014; Kromp, 1999; M. Loreau, 1984; Michel Loreau, 1983; McKemey, Symondson, Glen, & Brain, 2001; Mitchell, 1963; Pakarinen, 1994; Poulin & O'Neil, 1969; Ribera, Foster, Downie, McCracken, & Abernethy, 1999; Scherney, 1960, 2003; Sergeyeva & Gryuntal, 1990; W. O. Symondson, 2004; W. O. C. Symondson, 1989; W. O. C. Symondson, Glen, Wiltshire, Langdon, & Liddell, 1996; W. O. C. Symondson & Liddell, 1993, 1996; Tod, 1973; and Zhavoronkova, 1969.

Species name
Abax parallelepipedus
Abax parallelus
Amara aulica
Amara lunicollis
Amara similata
Anchomenus dorsalis
Anisodactylus
Anisodactylus binotatus
Broscus cephalotes
Calathus erratus
Calathus fuscipes
Calathus luctuosus
Calathus melanocephalus
Calathus micropterus
Calathus rotundicollis
Calosoma inquisitor
Carabus arvensis
Carabus auratus
Carabus auronitens
Carabus cancellatus
Carabus convexus
Carabus coriaceus
Carabus granulatus
Carabus hortensis

Carabus monilis
Carabus nemoralis
Carabus problematicus
Carabus violaceus purpurascens
Chlaeniellus nigricornis
Cychrus caraboides
Harpalus latus
Harpalus tardus
Laemonestus terricola
Licinus depressus
Molops piceus
Nebria brevicollis
Nebria salina
Poecilus cupreus
Poecilus lepidus
Poecilus versicolor
Pseudoophonus rufipes
Pterostichus anthracinus
Pterostichus cristatus
Pterostichus kugelannii
Pterostichus macer
Pterostichus madidus
Pterostichus melanarius
Pterostichus niger
Pterostichus nigrita
Pterostichus oblongopunctatus
Semiophonus signaticornis
Trechus gr. Quadristriatus
Trechus secalis

REFERENCES

Bohan, D. A., Bohan, A. C., Glen, D. M., Symondson, W. O., Wiltshire, C. W., & Hughes, L. (2000). Spatial dynamics of predation by carabid beetles on slugs. *Journal of Animal Ecology*, *69*(3), 367–379.

Brandmayr, P., & Brandmayr, T. Z. (1986). Food and feeding behaviour of some *Licinus* species (Coleoptera Carabidae Licinini). *Monitore Zoologico Italiano-Italian Journal of Zoology*, *20*(2), 171–181.

Cornic, J. F. (1973). Etude du regime alimentaire de trois especes de Carabiques et de ses variations en verger de pomiers. *Ann. Soc. Ent. France*, *9*, 69–87.

Dajoz, R. (2002). *The Coleoptera. Carabids and tenebionids: ecology and biology.* Éditions Tec & Doc.

Davies, M. J. (1953). The contents of the crops of some British carabid beetles. *Entomologist's Monthly Magazine*, *89*, 18–23.

Dennison, D. F., & Hodkinson, I. D. (1983). Structure of the predatory beetle community in a woodland soil ecosystem. I. Prey selection. *Pedobiologia*, *25*(2), 109–115.

Fawki, S., & Toft, S. (2005). Food preferences and the value of animal food for the carabid beetle *Amara similata* (Gyll.)(Col., Carabidae). *Journal of Applied Entomology*, *129*(9-10), 551–556.

Grimm, B., Paill, W., & Kaiser, H. (2000). The" Spanish slug": autecology, predators and wild plants as food plants. *Förderungsdienst*, *48*(1), 11–16.

Gruntal, S. Y., & Sergeyeva, T. K. (1989). Food relations characteristics of the beetles of the genera *Carabus* and *Cychrus*. *Zoologicheskij Zhurnal. Moscow*, *58*(1), 45–51.

Henderson, I. F., Andino, D., Peairs, E., Mazier, F., López, C., Cantoral Flores, O., … Bhat, P. K. (1996). *Slug and snail pests in agriculture. Monograph No. 66.* British Crop Protection Council, Surrey (RU).

Holland, J. M. (2002). *The agroecology of carabid beetles.* Intercept Limited.

Jelaska, L. S., Franjevic, D., JelASKA, S. D., & Symondso, W. O. (2014). Prey detection in carabid beetles (Coleoptera: Carabidae) in woodland ecosystems by PCR analysis of gut contents. *European Journal of Entomology*, *111*(5), 631.

Kromp, B. (1999). Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems & Environment*, *74*(1), 187–228.

Loreau, M. (1984). Etude experimentale de l'alimentation de *Abax ater* Villers, *Carabus problematicus* Herbst et *Cychus attenuatus* Fabricus (Coleoptera: Carabidae). *Annales de La Societe Royale Zoologique de Belgique*, *114*, 227–240.

Loreau, Michel. (1983). Le régime alimentaire de huit carabides (Coleoptera) communs en milieu forestier. *Acta Oecologica. Oecologia Generalis*, *4*(4), 331–343.

McKemey, A. R., Symondson, W. O. C., Glen, D. M., & Brain, P. (2001). Effects of slug size on predation by *Pterostichus melanarius* (Coleoptera: Carabidae). *Biocontrol Science and Technology*, *11*(1), 81–91.

Mitchell, B. (1963). Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). *The Journal of Animal Ecology*, 377–392.

Pakarinen, E. (1994). The importance of mucus as a defence against carabid beetles by the slugs *Arion fasciatus* and *Deroceras reticulatum*. *Journal of Molluscan Studies*, *60*(2), 149–155.

Poulin, G., & O'Neil, L. G. (1969). Observations sur les prédateurs de la limace noire, *Arion ater* (L.) (Gastéropodes, Pulmonés, Arionidés). *Phytoprotection*, *50*, 1–6.

Ribera, I., Foster, G. N., Downie, I. S., McCracken, D. I., & Abernethy, V. J. (1999). A comparative study of the morphology and life traits of Scottish ground beetles (Coleoptera, Carabidae). *Annales Zoologici Fennici*, 21–37.

Scherney, F. (1960). Beiträge zur Biologie und ökonomischen Bedeutung räuberisch lebender Käferarten. *Journal of Applied Entomology*, *47*(1-4), 231–255.

Scherney, F. (2003). *Unsere Laufkäfer: ihre Biologie und wirtschaftliche Bedeutung*. Westarp Wissenschaftenverlagsgesellschaft.

Sergeyeva, T. K., & Gryuntal, S. Y. (1990). Relationships of ground beetles, *Pterostichus*, species wiht their food resources. *Entomological Review (USA)*.

Symondson, W. O. (2004). Coleoptera (Carabidae, Staphylinidae, Lampyridae, Drilidae and Silphidae) as predators of terrestrial gastropods. *Natural Enemies of Terrestrial Molluscs. Oxford, UK, CAB International*, 37–84.

Symondson, W. O. C. (1989). Biological control of slugs by carabids. In *Henderson, I. F. (ed.) Slugs and Snails in World Agriculture, BCPC Monograph 41. British Crop Protection Council, Surrey, UK.* (pp. 295–300).

Symondson, W. O. C., Glen, D. M., Wiltshire, C. W., Langdon, C. J., & Liddell, J. E. (1996). Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *Journal of Applied Ecology*, 741–753.

Symondson, W. O. C., & Liddell, J. E. (1993). The detection of predation by *Abax parallelepipedus* and *Pterostichus madidus* (Coleoptera: Carabidae) on Mollusca using a quantitative ELISA. *Bulletin of Entomological Research*, *83*(4), 641–647.

Symondson, W. O. C., & Liddell, J. E. (1996). A species-specific monoclonal antibody system for detecting the remains of field slugs, *Deroceras reticulatum* (Muller)(Mollusca: Pulmonata), in carabid beetles (Coleoptera: Carabidae). *Biocontrol Science and Technology*, *6*(1), 91–100.

Tod, M. E. (1973). Notes on beetle predators of molluscs. *Entomologist*, *106*(1324), 196–201.

Zhavoronkova, T. N. (1969). Certain structural peculiarities of the Carabidae (Coleoptera) in relation to their feeding habits. *Entomological Review*, *48*, 462–471.

1422x691mm (72 x 72 DPI)