Green desert?: Biodiversity patterns in forest plantations

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ARTICLE INFO

ABSTRACT

Forest plantations represent a globally important land use, and their growth is expected to triple by the end of the century. Therefore, they could represent an important habitat remnant to support the survival of species. We measured the impact of forest plantations on biodiversity with a focus on eight groups of biota including saproxylic and ground mycorrhizal fungi, lichens, herbs together with shrubs, tree seedlings, aculeate hymenopterans, beetles and birds, in patches with formerly continuous vegetation dominated by native oak and in patches in spruce plantations (reflecting spatiotemporal discontinuity) in the East-Bohemian woodlands of the Czech Republic.

We found that species richness and numbers of obligate species were higher in native than in nonnative forests, but there was no significant difference in red-listed species. Nevertheless, the species of three of the eight studied groups profited from increasing proportion of spruce in the tree composition; only beetles and birds were negatively affected.

The results revealed more highly contrasting and often complex responses among the groups than what might be expected theoretically. The first key issue in the management of plantation forests in terms of biodiversity is the partial retention and restoration of islands of native vegetation. The second issue is that the impact of a nonnative tree species is not always negative.

1. Introduction

The conservation and maintenance of biodiverse forest ecosystems is a crucial issue worldwide. Importantly, the current global tree plantation area (excluding palm oil plantations) is approximately 7% of the forested area of the world, and this value is expected to grow to more than 20% over the next century (Brockerhoff et al., 2013; Hansen et al., 2013). At least one-quarter of the global commercial plantations consist of nonnative and fast-growing tree species (FAO, 2010). Moreover, natural forests will likely become fragmented and smaller with an accompanying decrease in their native biodiversity (McGill et al., 2015). The maintenance of biodiversity is not only an issue for conservation hot spots; it also applies to the harvested forests of Europe, North America and East Asia (Hansen et al., 2013; Hannah et al., 1995). Many of the old-growth beech and oak forests in central Europe have been transformed into plantations of coniferous trees, but the forest cover area in Europe is constantly increasing. The problem is that the

increase in forest cover is mainly attributable to the establishment of commercial plantation forests on former agricultural land (Forest Europe UN & FAO, 2011).

Plantation forests are often characterized by the public, journalists and, frequently, conservation biologists, as "biological deserts" or "green deserts" (Acosta, 2011; Qiu, 2014). Recently, it was estimated that biological deserts constitute 40% worldwide, and this value continues to increase (e.g., Polovina et al., 2008). The alteration of tree species in commercial plantation forests, especially through the introduction of nonnative trees, is predicted to hinder the survival of native organisms. Thus, the biodiversity of these forests is often considered to be very low, and it is claimed that they leave no place for rare or endangered species (Acosta, 2011; Graves, 2015). However, recent studies suggest that plantation forests are not necessarily green deserts (Carnus et al., 2006; Brockerhoff et al., 2008; Graves, 2015).

Indeed, biodiversity in forest plantations is not necessarily low relative to other systems. Changes to spatiotemporal heterogeneity (e.g.,

opening canopies or establishing an even-aged structure matrix) together with natural disturbances in forest plantations (e.g., leaving dead wood materials within the stands) at the landscape scale may help restore forest biodiversity (Lindenmayer et al., 2010; Horak et al., 2014). Leaving natural or seminatural patches within plantations to function as biodiversity islands may also be a useful strategy (As, 1993), and scattered veteran trees can be enormously important for retaining biodiversity (Horák, 2017).

Forest management may affect populations of species directly through logging and indirectly through changes in habitat heterogeneity and prey availability (Brunet et al., 2010). From the perspective of biodiversity, studying taxa with different life characteristics and strategies (Jackson and Fahrig, 2015) appears to be crucial, especially for plantation forests. Even when focusing on a particular taxa, different species require variety of habitat types (Horak et al., 2014), and plantation forests may represent an important habitat remnant to support the survival of such species. Plantation forests, therefore, should also be included in discussions of biodiversity-promoting natural disturbances (Lindenmayer et al., 2010).

We measured the impact of commercial forest plantations on biodiversity with a focus on multiple groups of biota. We used eight groups of organisms with disparate dispersal abilities, taxonomic affiliations and ecological requirements that we organized according to the disparate environmental characteristics that, to the best of our knowledge, reflect the conditions of plantation forests globally.

1.1. Objectives

We were interested in the effects of native vs. nonnative tree species on the biota in plantation forests. Our particular questions were:

 (i) Are there differences between native oak stands and nonnative spruce plantations in terms of species richness and the number of obligate and threatened species?
 (ii) What is the response of the species composition to the studied environmental variables?
(iii) What is the response of individual species to the studied environmental variables?

2. Materials and methods

2.1. Study area

The studied forests comprised nearly 6500 ha in a spatially continuous area of the East-Bohemian woodlands in the Czech Republic (GPS of centroid: 50.0260N, 16.1260E). In the past, this area was covered by temperate broadleaved forests dominated by sessile oak (*Quercus petraea*), but a large area has been planted for more than two centuries with the fast-growing, nonnative Norway spruce (*Picea abies*) that is only native to the highest mountains in central Europe. The oak stands served as isolated islands and represented the former dominant vegetation in the landscape, whereas the spruce plantations are nonnative trees and represented spatial and temporal discontinuity of former vegetation. In total, thirty mature stands distributed throughout the entire East-Bohemian woodlands were studied using a paired design with the minimal distance between sampling points and the distance from sampling points to the woodland edge set as 50 m.

2.2. Sampling

We used equal-stratified sampling (Hirzel and Guisan, 2002). Eight groups of organisms were selected for this study including two groups of fungi. Saproxylic fungi (i) are strictly associated with dead wood and may be sensitive to logging. Ground mycorrhizal fungi (ii) are relatively well known and mostly symbiotic with particular forest tree species, which mostly restricts them to forest habitat. We also sampled lichens

(iii) as specialized and sedentary symbiotic organisms. All the groups of fungi and lichens were collected during early autumn in 2014. We also sampled two groups of vascular plants, the first of which consisted of herbs and shrubs (iv) which were pooled together because forests had relatively few larger shrubs and many of these shrubs were low shrubs, such as Bilberry (*Vaccinium myrtillus*), with requirements similar to those of perennial plants. Herbs and shrubs belong to taxa with medium dispersal abilities. The second group of plants consisted of tree seedlings (v) produced via natural regeneration; the seeds of most forest trees have relatively high dispersal. We primarily studied this group because we predicted that the distribution of tree seedlings in mature stands would only be slightly affected by human disturbances and because seedlings accurately reflect the influence of oak and spruce on the future species composition of the stands. The plants were collected during late summer and early autumn in 2014. Hymenoptera (vi) were studied as invertebrate taxa with relatively good dispersal abilities, and they are also known to exhibit good responses to habitat alterations. Beetles (vii), along with hymenopterans, constitute one of the most species-rich taxa in the world, but their dispersal abilities are predicted to be lower than those of the hymenopterans. Aculeata Hymenoptera (excl. Formicidae) and Coleoptera (excl. Nitidulidae, Anobiidae, Chrysomelidae, Hydrophilidae, Leiodidae, Scirtidae and Throscidae) were collected during the vegetation growing season in 2011 and then identified to the species level. Birds (viii) were sampled as taxa that generally have relatively good dispersal abilities during spring 2014.

All of the studied insects were sampled using standard crossed panel window traps fixed to two iron sticks, which enabled the traps to move in the wind (Loskotová and Horák, 2016). All of the fungi, lichens, plants and birds were sampled within a 40-m radius surrounding the center of the stand (marked by the window trap) via a time-limited survey with 15 min as the limit for sampling (e.g., Horák et al., 2018a). In the case of fungi, lichens and plants, we used direct species observations; birds were also surveyed aurally (Horák et al., 2018a, 2018b).

2.3. Variables

We studied the total number of species. Obligate species were those that were only found in oak or spruce stands. We used obligate species instead of rare or infrequent species, which are more commonly analyzed, because rare species have a high potential to only be tourists. We also analyzed species listed on actual Czech red lists. All of these dependent variables were first analyzed with respect to the dominant tree species (spruce vs. oak). The species composition and individual species responses were then analyzed as a presence/absence matrix, which enabled a better final comparison among the different taxa.

We carefully selected four predictors that described the environmental conditions of the plantation forests. Not all stands were of regular shape, the same area, or pure spruce plantations or oak stands, so we measured (i) the percentage of spruce and oak within a 40-m radius (i.e., a circular patch) of the overstory. Spruce coverage exhibited collinearity with that of the oak (VIF = 2.26), meaning that an increasing amount of spruce reflected a decreasing amount of oak. Thus, the oak coverage was not analyzed further. We then analyzed the influence of spruce in the tree species composition. Additionally, (ii) we counted in detail all stumps less than five years old (reflected by the presence of bark) within a 40-m radius. Because we studied mature plantations of nearly the same age, the stumps had the same relative dimensions, and this predictor reflected the actual management intensity, which simply cannot be found in the management plans (e.g., due to sanitary cuttings). (iii) The third predictor was canopy openness, which reflected the microclimatic and light conditions of the individual patch being studied. Canopy openness was measured under the full foliage using fish-eye photographs from the center of a particular patch. (iv) The last predictor was chosen with respect to the potential edge effect and the effect of deforested land and measured as a percentage of

nonforest area within a 40-m radius.

2.4. Statistical analyses

All of the statistical analyses were performed in R 3.0.2 and CANOCO 4.5. The distribution of the dependent variables was tested with Shapiro-Wilk and chi-square tests, and the influence of the spatial autocorrelation was tested using Geary's C test under randomization (package spdep). The potential bias caused by the multicollinearity of the predictors was detected using the variance inflation factor (package HH). The Wilcoxon paired test was used to analyze the difference in the number of obligate and red-listed species between oak and spruce stands, and a canonical correspondence analysis (CCA) was used to investigate the species composition. The coordinates and their crossed and quadratic products were treated as continuous covariables for taxa that were significantly influenced by spatial autocorrelation (lichens and hymenopterans). A global permutation test was set at 9999 permutations under the full model; the permutation type was restricted for a split-plot design, and the whole plot was freely exchangeable. Because of the presence of empty samples for some taxa, we added one species present in all samples (Horak et al., 2014), and to estimate the response of the species richness gradient, we used the t-value of the correlated axis. We used generalized linear mixed-effect models (GLMM) with binomial distributions to analyze the response of individual species with site incidences exceeding 10. The pairs of plots were used as a random factor (package MASS). Each fish-eye photograph was evaluated on canopy openness using Gap Light Analyzer 2.0.

3. Results

We identified 789 species among the eight studied groups including 523 species of beetles, 71 bees and wasps, 50 saproxylic fungi, 49 herbaceous plants and shrubs, 37 birds, 21 lichens, 20 mycorrhizal fungi and 18 trees.

3.1. Species richness

We found that the number of species was significantly higher in native oak stands (76.81% of the total species) than in nonnative spruce stands (68.57%), and the number of obligate species in a particular group was also higher for oak (31.43%) than spruce (23.19%) stands (Fig. 1). In total, 30 species were listed on country red-lists, but we found no significant difference in the incidences of red-listed species between oak and spruce stands (z = 0.94; P = 0.35).

3.2. Species composition

The species composition of five of the eight studied groups responded significantly to the set of the studied independent predictors (Table SI 1). Beetles, hymenopterans, and birds exhibited the highest P-value significance followed by mycorrhizal fungi and tree seedlings. Wood-inhabiting fungi, lichens and plants were the only groups that did not respond to the studied environment.

Beetles, as medium-dispersing taxa, and birds, which are good dispersers, were negatively affected by increasing proportions of spruce in the tree composition (Table 1). Beetles also exhibited a complex pattern in response to the environment. In addition to the tree species composition, they also responded negatively to increasing canopy openness and were positively influenced by the surrounding deforested areas. Surprisingly, three groups benefited from an increasing percentage of spruce cover (Table 1) in contrast to previous results (Fig. 1). Namely, the number of species of mycorrhizal fungi that preferred spruce-dominated stands was higher than the number of species that were promoted by native oak. Tree seedlings constituted the second group that was positively influenced by spruce dominance, and bees and wasps responded positively to increases in the proportion of spruce and

canopy openness (Table 1).

3.3. Species responses

Three species (the lichen *Lepraria incana,* the beetle *Athous subfuscus,* and the bird *Fringilla coelebs*) should be regarded as generalists because they were represented in all study sites. Additionally, 1 species of fungi, 4 lichens, 2 trees, 5 bees and wasps, 17 beetles and 5 birds responded significantly to some of the studied environmental variables (Table SI 2). The fact that these 34 species responded to the environment suggests that research at the level of individual species could reveal some details about biodiversity that cannot be observed by analyzing groups.

Surprisingly, more species (17 in total) were positively influenced than were negatively affected (10 in total) when the proportion of spruce increased (Table SI 2). Moreover, many species were not affected by the nonnative trees in forests.

Regarding the other plantation forest parameters, most species (especially insects and their predators) responded positively to increasing sunlight in the stands. Indeed, increasing the area without forest cover negatively affected fewer species than the opposite, but the difference was not as large as that observed for canopy openness. More species preferred intermediate felling in the recent past in mature forests (Table SI 2).

4. Discussion

We found that there were differences between native oak stands and nonnative spruce plantations in terms of species richness and the number of obligate species, but this difference was not significant for threatened species. Six studied groups responded significantly to the studied independent variables regarding their species composition. We also found that 34 species responded to the studied environment.

4.1. Biodiversity and the impact of dominants

Based on the ability of oak stands to host higher numbers of unique and total species, the retention and future restoration of fragmented islands of native tree species appear to be highly important within plantation forest matrices (As, 1993; Rodríguez-San Pedro and Simonetti, 2015; Phillips et al., 2018).

4.2. Importance of tree species composition

The results for saproxylic fungi, lichens and plants were quite surprising because these groups are often studied with a number of bioindicators (Hermy et al., 1999; Padoa-Schippoa et al., 2006). Thus, it is difficult to describe plantation forests as green deserts for saproxylic fungi, lichens or plants, but the abilities of these groups to serve as indicators in this type of environment might be limited in comparison with forest reserves (e.g., Horák et al., 2018b).

From the perspective of a multitaxa approach, the impacts of plantation forests on biodiversity were more complex than what might have been expected at first glance. The finding that the representation of nonnative trees negatively impacted only two taxa was relatively surprising (Newbold et al., 2015), and in the case of the complex response of beetles, this effect may be explained by the interconnection of these species with plants and fungi and their dispersal abilities (Jackson and Fahrig, 2015; Müller et al., 2015). The effects on birds were especially surprising because this taxon consists, in general, of mobile animals (especially relative to the other studied taxa), but the dispersal abilities of some bird species might be very low or limited because of habitat specificity. For example, a conspicuous passerine, the Golden oriole (*Oriolus oriolus*), was only observed in oak stands. Trees and hymenopterans preferred large amounts of spruce, and a similar response was interesting in the case of fungi with mycorrhiza because
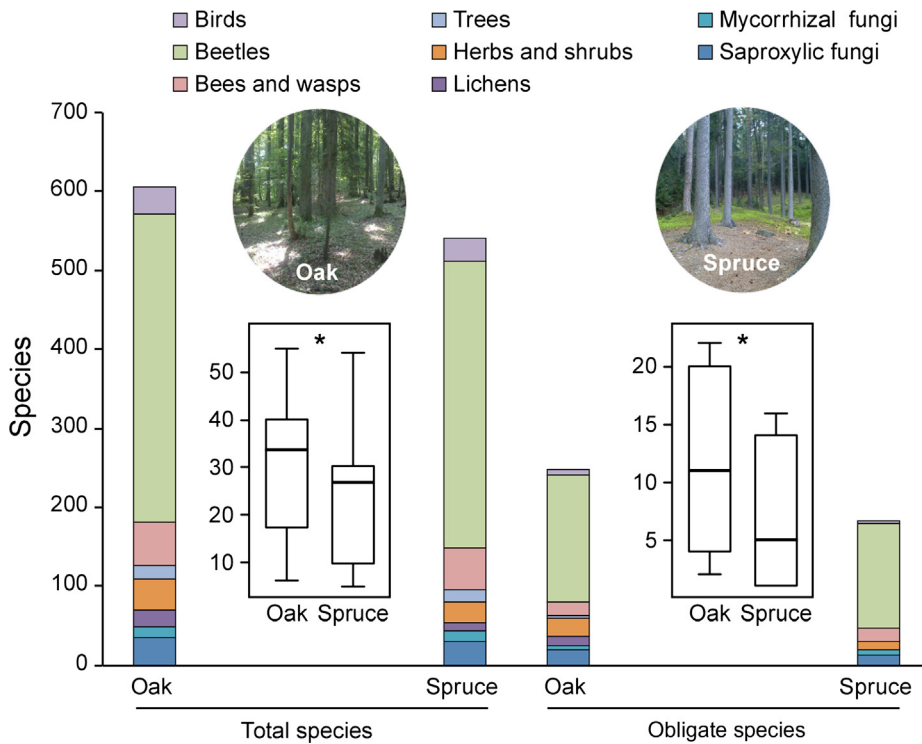
Fig. 1. Differences in the species richness of the studied groups. The differences between forest stands dominated by native (Sessile oak: yellow) and nonnative (Norway spruce: green) trees in temperate plantation forests are presented (*P < 0.05; outliers are not shown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Responses of five of the studied groups to the environmental variables. The response regarding the number of species was analyzed in temperate plantation forests using the t-value in CCA.

Group	Predictor	R^2 (%)	F	P	Response
Mycorrhizal fungi	Canopy openness	4.05	1.18	0.23	
	No forest	2.53	0.73	0.66	
	Spruce	6.94	2.08	< 0.001	+
	Stumps	4.14	1.21	0.28	
Trees	Canopy openness	4.46	1.28	0.18	
	No forest	3.81	0.96	0.54	
	Spruce	6.47	1.94	< 0.001	+
	Stumps	3.60	0.89	0.53	
Bees and wasps	Canopy openness	5.19	1.53	0.004	+
	No forest	4.39	1.31	0.13	
	Spruce	4.55	1.12	< 0.001	+
	Stumps	3.30	0.92	0.62	
Beetles	Canopy openness	4.42	1.19	0.016	–
	No forest	4.29	1.25	0.001	+
	Spruce	4.73	1.39	< 0.001	–
	Stumps	3.32	0.97	0.64	
Birds	Canopy openness	3.58	0.93	0.60	
	No forest	4.25	1.29	0.18	
	Spruce	7.47	2.27	< 0.001	–
	Stumps	3.94	1.00	0.44	

such fungi should be predicted to have poor dispersal relative to other taxa (Rasmussen and Rasmussen, 2009).

One important issue in nature conservation is natural habitat restoration, including in plantations and degraded forests (Lamb et al., 2005; McFadden and Dirzo, 2018). The higher number of seedlings in spruce stands in our research indicated that plantations of nonnative trees have a high potential for restoration through natural succession; that is, setting aside a few hectares of stands within the plantation matrix by forest managers would lead to the creation of seminatural patches and thus increase the landscape connectivity without incurring additional costs. These plantations have also been described as ecologically unstable (McCann, 2000; Brang et al., 2014; Veldman et al.,

2015), but bees and wasps, which were observed to prefer nonnative trees in our study, include a significant number of keystone species including pollinators of commercial plants and predators and parasites that function in pest management (Thies and Tscharntke, 1999). Given that these species were positively influenced by spruce and have relatively high mobility, we can conclude that the future improvement of plantation stability is promising (Cruz-Neto et al., 2018), especially if plantations could be incorporated into a more scattered forest landscape (McCann, 2000).

4.3. Disentangling the contrast

The known beneficial effect of habitat matrices on biodiversity (Horák et al., 2014; Redon et al., 2014; Mortelliti et al., 2015) likely explains why our results appeared to be contrasting and why this factor represents an opportunity to ensure the future of plantation forests (Rodríguez-San Pedro and Simonetti, 2015; Cruz-Neto et al., 2018). We found that stands dominated by native tree species hosted a higher number of species, including those exclusive to native habitats, so we can conclude that the remnants of the former forest vegetation types, even when managed for timber products, promoted biodiversity in plantation forests. Therefore, the maintenance of the former vegetation, at least as habitat islands, is a key opportunity for plantation forests (Hanzelka and Reif, 2016).

Nevertheless, increasing the representation of nonnative conifer species appeared to benefit several groups and species. Thus, we can conclude that mixtures of different species in plantation forests could benefit biodiversity, and whether the mixed species stands are native matters little. Thus, each tree species contributes some spatial and species-specific diversity to the organismal distribution (Müller et al., 2015). Additionally, more heterogeneous plantation forests can be predicted to be more resistant to natural disturbances (Verheyen et al., 2016) and thus more sustainable (e.g., because of diverse forms of carbon sequestration; Joźefowska et al., 2017). For example, spruces are used by many generalists but can also attract specialists from mountainous forests (Röder et al., 2010).

There are two possible approaches for maintaining and improving

biodiversity in plantations:

(1) Increasing the heterogeneity of tree species within the stands (i.e., at a spatial scale of a few hectares), which is important for appropriate individual forest management, and
(2) Maintaining native vegetation inside the matrix of plantation forests (i.e., the landscape spatial scale), which is important for global forest management.

4.4. Implications for promoting biodiverse plantations

We highlighted the important role of native vegetation as habitat islands within plantations; these fragments could host higher numbers of unique and total species. We also focused on the effect of the representation of nonnative trees in plantations, and despite their poor reputation among nature conservationists, these species appeared to have few negative impacts. Furthermore, some groups even benefited from them. Thus, plantations of nonnative trees are not always green deserts and we can expect similar patterns of biodiversity elsewhere. These conclusions are strengthened by the fact that we studied eight groups with disparate dispersal abilities, taxonomic affiliations and ecological requirements and combined them with diverse environmental characteristics reflecting the conditions of forest plantations worldwide.

The first key issue in promoting the biodiversity of plantation forests during their expected future expansion is the retention and restoration of native vegetation. The second issue is the representation of nonnative trees in various mixtures.

We believe that this study contributes to the knowledge of biodiversity because plantation forests will be a dominant land use type in the future (FAO, 2010). Thus, plantations that are designed to better deliver socioeconomic benefits (e.g., recreation and relaxation activities) and nonproductive forest functions (e.g., dust reduction, and mushroom and fruit production) while providing ecological services (e.g., biodiversity maintenance) will be very important in the future.

Acknowledgments

Funding

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.019.

References

Acosta, I., 2011. Green Desert' Monoculture Forests Spreading in Africa and South America. The Guardian. http://www.theguardian.com/environment/2011/sep/26/monoculture-forests-africa-south-america.

As, S., 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. Ecography 16, 219–228. https://doi.org/10.1111/j.1600-0587.1993.tb00212.x.

Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, C., et al., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87, 492–503. https://doi.org/10.1093/forestry/cpu018.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F.B., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. Forest Ecol. Manag. 301, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951. https://doi.org/10.1007/s10531-008-9380-x.

Brunet, J., Fritz, O., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. Ecol. Bull. 53, 77–94.

Carnus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., et al., 2006. Planted forests and biodiversity. J. For. 104, 65–77.

Cruz-Neto, O., Silva, J.L. Se, Woolley, M.M., Tabarelli, M., Lopes, A.V., 2018. Pollination partial recovery across monospecific plantations of a native tree (Inga vera, Leguminosae) in the Atlantic forest: Lessons for restoration. Forest Ecol. Manag. 427, 383–391. https://doi.org/10.1016/j.foreco.2018.06.023.

FAO, 2010. Global forest resources assessment 2010 – main report. FAO Forestry. Rome, Paper 163.

Forest Europe, U.N., F.A.O., 2011. State of Europe's Forests 2011. Status and Trends in Sustainable Forest Management in Europe. Forest Europe Liaison Unit, Oslo.

Graves, G.R., 2015. Recent large-scale colonisation of southern pine plantations by Swainson's warbler Limnothlypis swainsonii. Bird Conserv. Int. 25, 280–293. https://doi.org/10.1017/S0959270914000306.

Hannah, L., Carr, J.L., Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers. Conserv. 4, 128–155. https://doi.org/10.1007/BF00137781.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., et al., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Hanzelka, J., Reif, J., 2016. Effects of vegetation structure on the diversity of breeding bird communities in forest stands of non-native black pine (Pinus nigra A.) and black locust (Robinia pseudoacacia L.) in the Czech Republic. Forest Ecol. Manag. 379, 102–113. https://doi.org/10.1016/j.foreco.2016.08.017.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol. Conserv. 91, 9–22. https://doi.org/10.1016/S0006-3207(99)00045-2.

Hirzel, A., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecol. Model. 157, 331–341.

Horák, J., 2017. Insect ecology and veteran trees. J. Insect Conserv. 21, 1–5. https://doi.org/10.1007/s10841-017-9953-7.

Horák, J., Pavlíček, J., Kout, J., Halda, J.P., 2018a. Winners and losers in the wilderness: response of biodiversity to the abandonment of ancient forest pastures. Biodivers. Conserv. 27, 3019–3029. https://doi.org/10.1007/s10531-018-1585-z.

Horák, J., Rom, J., Rada, P., Šafářová, L., Koudelková, J., Zasadil, P., et al., 2018b. Renaissance of a rural artifact in a city with a million people: biodiversity responses to an agro-forestry restoration in a large urban traditional fruit orchard. Urban Ecosyst. 21, 263–270. https://doi.org/10.1007/s11252-017-0712-z.

Horak, J., Vodka, S., Kout, J., Halda, J.P., Bogusch, P., Pech, P., 2014. Biodiversity of most dead wood-dependent organisms in thermophilic temperate oak woodlands thrives on diversity of open landscape structures. Forest Ecol. Manage. 315, 80–85. https://doi.org/10.1016/j.foreco.2013.12.018.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. https://doi.org/10.1111/geb.12233.

Józefowska, A., Pietrzykowski, M., Woś, B., Cajthaml, T., Frouz, J., 2017. The effects of tree species and substrate on carbon sequestration and chemical and biological properties in reforested post-mining soils. Geoderma 292, 9–16. https://doi.org/10.1016/j.geoderma.2017.01.008.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632. https://doi.org/10.1126/science.1111773.

Lindenmayer, D.B., Likens, G.E., Franklin, J.F., 2010. Rapid responses to facilitate ecological discoveries from major disturbances. Front. Ecol. Environ. 8, 527–532. https://doi.org/10.1890/090184.

Loskotová, T., Horák, J., 2016. The influence of mature oak stands and spruce plantations on soil-dwelling click beetles in lowland plantation forests. PeerJ 4, e1568. https://doi.org/10.7717/peerj.1568.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233. https://doi.org/10.1038/35012234.

McFadden, T.N., Dirzo, R., 2018. Opening the silvicultural toolbox: a new framework for conserving biodiversity in Chilean timber plantations. Forest Ecol. Manag. 425, 75–84. https://doi.org/10.1016/j.foreco.2018.05.028.

McGill, B.J., Dornelas, M., Gotelli, N.J., Magurran, A.E., 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends Ecol. Evol. (Amst.) 30, 104–113. https://doi.org/10.1016/j.tree.2014.11.006.

Mortelliti, A., Michael, D.R., Lindenmayer, D.B., 2015. Contrasting effects of pine plantations on two skinks: results from a large-scale 'natural experiment. Anim. Conserv. 18, 433–441. https://doi.org/10.1111/acv.12190.

Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., et al., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. J. Appl. Ecol. 52, 753–762. https://doi.org/10.1111/1365-2664.12421.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., et al., 2015.

Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.

Padoa-Schioppa, E., Baietto, M., Massa, R., Bottoni, L., 2006. Bird communities as bioindicators: the focal species concept in agricultural landscapes. Ecol. Indic. 6, 83–93. https://doi.org/10.1016/j.ecolind.2005.08.006.

Phillips, H.R.P., Halley, J.M., Urbina-Cardona, J.N., Purvis, A., 2018. The effect of fragment area on site-level biodiversity. Ecography 41, 1220–1231. https://doi.org/10.1111/ecog.02956.

Polovina, J.J., Howell, E.A., Abecassis, M., 2008. Ocean's least productive waters are expanding. L03618–LL03618. Geophys. Res. Lett. 35. https://doi.org/10.1029/2007GL031745.

Qiu, L., 2014. Rare southern songbird thrives in 'Biological Deserts'. National Geographic. < http://news.nationalgeographic.com/2014/11/141113-warbler-pines-timber-animals-birds-environment > .

Rasmussen, H.N., Rasmussen, F.N., 2009. Orchid mycorrhiza: implications of a mycophagous life style. Oikos 118, 334–345. https://doi.org/10.1111/j.1600-0706.2008.17116.x.

Redon, M., Luque, S., Gosselin, F., Cordonnier, T., 2014. Is generalisation of uneven-aged management in mountain forests the key to improve biodiversity conservation within forest landscape mosaics? Ann. Forest Sci. 71, 751–760. https://doi.org/10.1007/s13595-014-0371-7.

Röder, J., Bässler, C., Brandl, R., Dvořak, L., Floren, A., Goßner, M.M., et al., 2010. Arthropod species richness in the Norway Spruce (Picea abies (L.) Karst.) canopy along an elevation gradient. Forest Ecol. Manag. 259, 1513–1521. https://doi.org/10.1016/j.foreco.2010.01.027.

Rodríguez-San Pedro, A., Simonetti, J.A., 2015. The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter? Landscape Ecol. 30, 1561–1572. https://doi.org/10.1007/s10980-015-0213-5. Acosta.

Thies, C., Tscharntke, T., 1999. Landscape structure and biological control in agroecosystems. Science 285, 893–895. https://doi.org/10.1126/science.285.5429.893.

Veldman, J.W., Overbeck, G.E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G.W., et al., 2015. Where tree planting and forest expansion are bad for biodiversity and ecosystem services. BioScience. BioScience 65, 1011–1018. https://doi.org/10.1093/biosci/biv118.

Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., et al., 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. Ambio 45, 29–41. https://doi.org/10.1007/s13280-015-0685-1.