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Non-native tree species (Pseudotsuga menziesii) strongly decreases predator biomass and abundance in mixed-species plantations of a tree diversity experiment

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ABSTRACT

Stand diversification increasingly emerges as a promising means for improving the multi-functionality and sustainability of management in plantation forests. Increasing tree species richness might potentially also benefit natural enemies, which can substantially contribute to sustainable forest management via top-down control of forest pests. However, there is little empirical evidence on how tree species richness affects the diversity and abundance of predators, as the majority of analyses to date have rarely gone beyond comparisons of monocultures and two species mixtures. Here, we analyzed the performance of spiders as important generalist predators in a tree diversity experiment that uses four of the economically most important broadleaved and coniferous tree species in Europe. We tested the extent to which tree species richness and the identity of the planted tree species affect the abundance, biomass, species richness and functional diversity of spiders. Whereas tree species richness in general had no significant effect, tree species identity strongly affected spider biomass and abundance-with a particularly strong negative effect of the non-native Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). Our results indicate that increasing tree species richness does not necessarily promote characteristics of natural enemy assemblages relevant for pest control in forests and thus not all functions that may be important in a multi-functional management context. Rather, tree species composition and identity will often be of crucial importance in determining forest ecosystem functions and services. The fact that the severe impact of Douglas fir persisted even in diversified tree species mixtures suggests that stand-level predator efficiency can be reduced for tree species growing adjacent to or in mixture with this species. This calls for a more thorough examination of the ecological consequences of the increasing use of this species in forestry across Europe, in particular considering that climate change may increase the potential of pest outbreaks and thus the need for adequate control in the next decades.

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1. Introduction

The relationship between biodiversity and the provisioning of ecosystem functions and services has become a major focus of ecological research and is increasingly being integrated into economic decision making and environmental management schemes (Gómez-Baggethun et al., 2010; Cardinale et al., 2012; Ruckelshaus et al., 2014). Forest ecosystems, which provide key services essential to human well-being (Kremen et al., 2000; Bonan, 2008), have only relatively recently been incorporated more thoroughly into the biodiversity-ecosystem function and service framework (Scherer-Lorenzen et al., 2007). Several studies have shown not only increased biomass production, but also higher stability and insurance against biotic and abiotic disturbances, even with only moderate increases in tree species richness (e.g. Jactel and Brockerhoff, 2007; Morin et al., 2011; Gamfeldt et al., 2013; for a review see Scherer-Lorenzen, 2014). All of this may enhance the long-term economic value of forests (Knoke et al., 2008) and, moreover, promote the overall biodiversity of plants and animals associated with these forest ecosystems. This corresponds well with the goals of sustainable forest management approaches that are being pursued in many regions with a long history of intensive forest management, such as in Europe (Rametsteiner and Mayer, 2004; Wolfslehner et al., 2005). However, despite efforts of promoting the establishment of mixtures (usually two species mixtures) over the last decades, to date the largest proportion of forests even in Europe is still made up of monoculture plantations (Knoke et al., 2008).





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To create stronger incentives to re-evaluate traditional forest management practices, particularly regarding sustainable forest management, a better understanding may be required of how tree species diversity actually affects many of the vital functions and services provided by forests that have received little attention in this respect so far (Nadrowski et al., 2010).

A key function that is often considered to be positively associated with more diverse plant communities (Root, 1973; Haddad et al., 2009) and of high economic importance is pest control (Losey and Vaughan, 2006). Predators may benefit from increased resource and prey diversity in more diverse plant communities (Root, 1973; Haddad et al., 2009) and thus contribute to the reduction of herbivore damage and pest outbreaks often observed with an increase in the tree diversity of forest stands (Jactel and Brockerhoff, 2007; Castagneyrol et al., 2014). The role of predators in stabilizing forest ecosystem functioning by controlling herbivores is particularly relevant considering that climate change will increase the risk of pest outbreaks and facilitate the immigration and establishment of exotic pest species in the next decades (Dale et al., 2001; Lindner et al., 2010; Netherer and Schopf, 2010). However, whether tree diversity actually promotes predator effects under real-world conditions is far from clear (Zhang and Adams, 2011). There are comparatively few studies on the relationship between tree diversity and the abundance and diversity of predators that went beyond comparisons of monocultures and two species mixtures. Those that did found either positive (e.g. Sobek et al., 2009), negative (Schuldt et al., 2011; Zou et al., 2013), or no clear effects on predators (Schuldt et al., 2008; Vehviläinen et al., 2008). In the latter case, tree species composition and species identity were often found to have stronger effects than tree species richness per se (Zhang and Adams, 2011). The observational character of most of these studies, with varying degrees of environmental variation among study locations, could be one of the reasons for the heterogeneous results.

Here, we make use of a controlled tree diversity experiment with early successional forest that is based on tree species of high economic importance to forestry in Central Europe. We test for the effects of tree species richness and species identity on the abundance, biomass and diversity of a functionally important group of generalist predators, epigeic spiders (Symondson et al., 2002). Epigeic predators have been shown to be able to strongly affect the densities of forest pests, many of which spend part of their life cycle in the forest floor stratum (e.g. Tanhuanpää et al., 1999). Most previous studies analyzing plant diversity effects on predators have focused on predator abundance and species richness. However, the functional impact and thus the pest-control potential of predators may be more strongly determined by their biomass and functional diversity (Saint-Germain et al., 2007; Schmitz, 2009; Reiss et al., 2011), and we thus include these two assemblage characteristics for a more comprehensive analysis. The experimental design with up to four tree species planted in mixture well represents large-scale forest diversity in the temperate and boreal parts of Europe (see e.g. Gamfeldt et al., 2013). A mix of broadleaved and coniferous species as well as the inclusion of a nonnative tree species that has become the economically most important exotic tree species in Europe (Douglas fir; Schmid et al., 2014) reflects two important trends in forest management practices that are in need of further exploration in the framework of biodiversity and ecosystem function research. Considering that plant species richness may increase the diversity of resources and prey (Root, 1973; Haddad et al., 2009) and that non-native tree species might provide generalist predators with less diverse prey (Goßner and Ammer, 2006), we hypothesize that (i) tree species richness promotes the abundance, biomass, species richness and functional diversity of spiders, and thus the pest-control potential of forest stands, and that (ii) tree species identity plays an important additional role in structuring spider assemblages in that (locally) non-native conifers may decrease spider diversity and abundance (in particular of typical forest species).

2. Materials and methods

2.1. Study site and experimental design

The study was conducted on the 'Kaltenborn' site of the BIO-TREE tree diversity experiment (Scherer-Lorenzen et al., 2007) in southwest Thuringia, Germany (50°47' N, 10°13' E). The study site is located on acidic bedrock at a height of 320–350 m a.s.l. It is characterized by a subatlantic climate, with a mean annual temperature of 7.8 °C and a mean annual precipitation of 650 mm (Scherer-Lorenzen et al., 2007).

Details on the experiment, designed to study the relationships between tree species richness and ecosystem functions, are provided by Scherer-Lorenzen et al. (2007). In short, the experimental setup at the 'Kaltenborn' site consists of 16 study plots of 0.58 ha (120 m \times 48 m), established in 2003/2004 and thus representing early successional forest, which cover a total area of 20 ha under homogeneous site conditions directly adjacent to a pine-beech forest. The 16 study plots comprised of the monocultures (4 plots), all possible two (six plots) and three species mixtures (four plots), and the four species mixture (2 plots) of four tree species: the broadleaved, deciduous European beech (Fagus sylvatica L.) and sessile oak (Quercus petraea Liebl.), and the coniferous Norway spruce (Picea abies (L.) H. Karst.) and Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). While the latter is an exotic species, all four tree species are commonly found in the surrounding forests and economically highly important for local forestry. Diversity treatments were randomly allocated across the 16 plots of the study site. Within each plot, tree species were planted in monospecific patches of $8 \text{ m} \times 8 \text{ m}$ (the size of these patches being based on the canopy properties of full-grown tree individuals), with the aim of retaining one tree individual per species-specific patch in the long term while avoiding outcompetition of slow-growing species at the early stage of the experiment. Tree individuals were planted in rows of 2 m distance, with the distance within rows following common planting practice (2 m for the two conifers, 1 m for the two deciduous species). Each plot was divided into three subplots that will receive different treatments in the future (unmanaged, managed, managed with addition of further tree species; see Scherer-Lorenzen et al., 2007). For details on plot conditions, see Table S1 (Appendix A).

2.2. Spider data and plot characteristics

Spiders were captured with pitfall traps, which were exposed over the main growing season in 2012 (17 April – 02 October) and emptied every 3 weeks. Five traps (0.5 L plastic cups with an upper diameter of 9.5 cm) were installed in each of the 16 study plots and filled with 0.15 L of a preserving solution (40% ethanol, 30% water, 20% glycerol, 10% acetic acid, and a few drops of detergent to reduce surface tension). The traps were arranged in a $16 \text{ m} \times 16 \text{ m}$ square in the center of the unmanaged subplots, with one trap in each of the four corners and the fifth trap in the center of the square. The square's corners were arranged such that each trap was located at the intersection of four neighboring monospecific planting patches (with all four patches of the same species in monocultures and up to four different species in the most diverse mixtures). This ensured that each trap was positioned at a location that represented a mix of the environmental conditions associated with each of the tree species planted in a given plot.

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