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Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment

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Citation: Hantsch, L., U. Braun, M. Scherer-Lorenzen, and H. Bruelheide. 2013. Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment. Ecosphere 4(7):81. http://dx.doi.org/10.1890/ES13-00103.1

Abstract. Current theory on transmission rates of plant pathogens predicts a strong influence of host richness on the degree of infection. In addition, identity effects, caused by the presence of particular species in a community, may also drive biodiversity and ecosystem functioning relationships, with "selection" or "sampling effects" being particularly important. We tested the effect of tree species richness and tree species identity effects on foliar fungal pathogens on four forest tree species of the temperate zone making use of the BIOTREE tree diversity experiment in Germany. We hypothesized that fungal species richness is positively and fungal pathogen load negatively related to tree species richness. In addition, we tested whether species number of foliar biotrophic fungi and pathogen load depend on tree community composition and on the presence or absence of particular disease-prone tree species. All foliar fungi were identified macro- and microscopically and subjected to statistical analyses at three hierarchical levels, at the *plot level*, the level of single *tree species* and the level of individual *fungus species*. There was a negative effect of tree richness on the pathogen load of common powdery mildew species. Moreover, we found strong tree species identity effects at the *plot level* as the presence of *Quercus* resulted in a high pathogen load. Thus, for the first time we experimentally showed that disease risk and pathogen transmission of foliar fungal pathogens in temperate forest tree ecosystems may depend on tree richness and on the presence of particular disease-prone species.

Key words: biodiversity and ecosystem functioning; BIOTREE experiment; disease dilution effect; ecosystem processes; *Erysiphales*; *Fagus sylvatica*; local neighborhood; *Quercus*; Shannon diversity; tree species identity effects; tree species richness effects.

Received 22 March 2013; revised and accepted 3 June 2013; **published** 18 July 2013. Corresponding Editor: M. Allen.

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Introduction

It has been hypothesized that biodiversity is able to reduce passive pathogen transmission by different mechanisms, such as host distance and abundance, pathogen behavior and the environmental conditions shaped by hosts and non-hosts (Keesing et al. 2006, 2010). Pathogen transmission rates are one of a multitude of ecosystem processes that might be affected by biodiversity (Loreau et al. 2001, Hooper et al. 2005, Balvanera et al. 2006). Furthermore, biodiversity might affect the average susceptibility of individuals in the community, by influencing the ability to resist pathogen attacks (Shurtleff and Averre 1997: 321). Less susceptible individuals will

result in lower community dynamics, thus causing more stable communities (Pautasso et al. 2005). The disease-diversity hypothesis states that high species or high genetic diversity in a community confers disease resistance (Heybroek 1982, Burdon 2001).

At the community scale, the *plot level*, there might be different mechanisms that result in such diversity effects. For example, a drier microclimate in mixtures than in monocultures has been found to be the cause for the decrease in fungal disease levels in experimental rice fields with genetically diverse mixtures of rice cultivars (Zhu et al. 2005). From the host species' perspective, lower levels of pathogen load would be considered positive, since an intact leaf area would provide a higher photosynthetic gain. As a fungal infection finally results in a higher mortality of single leaves or whole plants, and thus, presents a type of disturbance, a decreased pathogen load would finally be translated into a higher net primary production of the whole plant community (Mitchell 2003, Berger et al. 2007). Thus, biodiversity ecosystem functioning would be negatively affected by leaf pathogens, because flux rates of matter and energy in the system would be reduced (Jiang et al. 2008). In contrast, host species richness is expected to have positive effects on pathogen species richness, as a wider niche space is provided for the different pathogen species (Bond and Chase 2002). Positive or neutral biodiversity and ecosystem functioning effects on pathogen richness might also occur if additional plant species are important for completing the pathogens' life cycles (Cheatham et al. 2009, Johnson et al. 2009, Mundt et al. 2011). This is the case for many rust fungi (*Puccinia* spp.), which have a hetero-oecous life style and use different plant species as alternate hosts for sexual reproduction (Cheatham et al. 2009). Positive effects of host species richness are representing a parallel to the effect of "associational susceptibility" with respect to herbivory. In a meta-analysis of herbivore abundance and damage, Vehviläinen et al. (2007) showed that mixed stands received more damage than monocultures, mainly caused by generalist herbivores. Similarly, moose browsing tended to increase with the number of tree species in the mixture (Vehviläinen and Koricheva 2006).

In addition to host diversity effects, biodiversity and ecosystem functioning relationships at the community scale can be driven by identity effects, which could be caused by the presence of particular species in a community, with "selection" or "sampling effects" being particularly important (Loreau and Hector 2001). Positive or negative selection effects occur when, on average, species that perform accordingly higher or lower than average in the monoculture increase their relative abundance in diverse communities. In addition, sampling effects result from the increasing probability for a species with a particularly high or low contribution to ecosystem functioning to be present in species-rich communities (Loreau and Hector 2001).

Both diversity and identity effects do also occur at the scale of the local neighborhood, the *tree species level* and the *fungal species level*. Thus, the disease-diversity hypothesis can be extended to individual hosts, allowing comparing different host species in their degree of susceptibility as well as different fungal species in their degree of infectiousness. With increasing host species richness the transmission risk for a specialist fungal species will decrease because of a decreased host density in the local neighborhood (Fig. 1a). Then, particular tree species in the neighborhood might either increase or decrease the pathogen load of a target tree, thus having positive or negative effects on the hosts pathogen load (Fig. 1b). Both types of identity effects can be considered different cases of neighbor-mediated facilitation. The first case would be a neighbor-species mediated facilitation of the pathogen species, the latter a neighbor-species mediated facilitation of the host species. Such identity mechanisms have been demonstrated by sowing non-host plant species in grassland diversity experiments, which resulted in a decreased pathogen load (Mitchell et al. 2002). Similarly, Roscher et al. (2007) showed a reduction of disease intensity of rust fungi on the host species *Lolium perenne* with increasing species richness.

The question whether positive or negative selection effects prevail in a host-pathogen system depends on whether the system is dominated by susceptible or more resistant host species. It has recently been suggested that ecosystem functions involving more than one trophic level, such as host-pathogen systems,

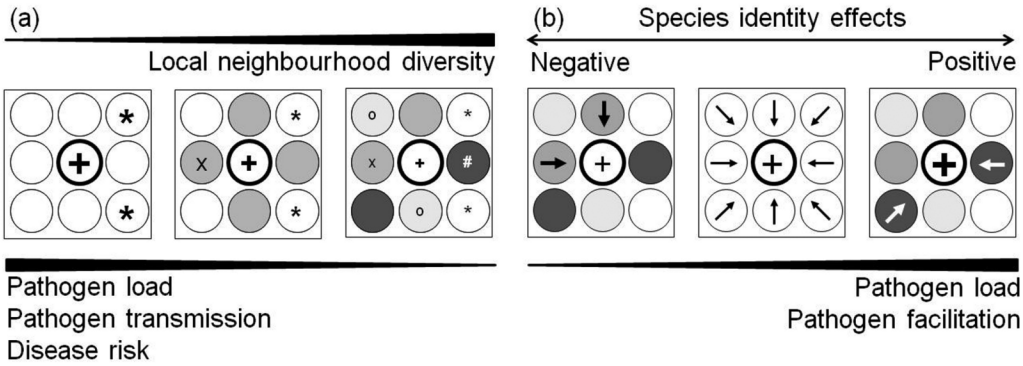

Fig. 1. Graphical illustration of how biodiversity can affect fungal pathogen richness and fungal pathogen load at the local neighborhood scale in experimental plant communities of constant plant species density. Plant individuals are represented by circles, with different colors being different species. Target individuals are marked by a thick black outline. The symbols in the circles represent specialized biotrophic fungal pathogens, with different symbols indicating different species and different size of symbols showing a different degree of pathogen load. Circles with arrows indicate that the plant species changes the local environment of a target species. (a) Host species richness effects resulting from a reduced pathogen transmission risk with increasing plant species richness. (b) Species identity effects brought about by particular plant species that might either increase or decrease the pathogen load of the target individual, depending on whether the species in the neighborhood changes the environmental conditions in a favorable or unfavorable manner for the specialized biotrophic pathogen.

might be predominantly characterized by negative selection effects (Jiang et al. 2008), because less susceptible host species might be dominant more often than susceptible ones. However, empirical evidence for this proposition is scarce and contradictory.

Pathogens do not only respond to host richness but do also have effects on host species performance and composition. They can, like other consumers (Duffy 2003), change the outcome of competition between host species (Mordecai 2011). Pathogens can promote coexistence among host species by regulating the relative abundance of hosts. According to the Janzen-Conell hypothesis, pathogens can cause local negative density dependence of host species, and thus, affect the spatial host abundance patterns (Janzen 1970, Connell 1971, Bagchi et al. 2010). However, the situation in most ecosystems might be even more complex, as beside hosts and pathogens further components are involved in food-webs (Duffy 2002). In general, biotic networks and the epidemiology of directly transmitted infectious diseases are fundamentally linked (Keeling and Eames 2005). This entanglement of factors and the confounding of causes and effects make it extremely difficult to analyze the relationship between host and pathogen species richness in observational studies. The obvious solution to this problem is an experiment in which host density is kept constant and host species richness is manipulated. Such tree diversity experiments have become available only recently (Verheyen 2012).

In this study we make use of the German tree diversity experiment BIOTREE (Scherer-Lorenzen et al. 2007). On the community scale, we tested the hypotheses that (1) the species number of foliar biotrophic fungi is positively and the pathogen load is negatively related to the host tree species richness. We also expected strong tree species identity effects and hypothesized that (2) species number of foliar biotrophic fungi and pathogen load depend on community composition and on the presence or absence of particular disease-prone tree species. With focus on the local neighborhood scale, we tested (3) whether pathogen load is negatively related to the tree species richness (Fig. 1a) and (4) to the presence or absence of particular tree species (Fig. 1b).

To our knowledge this is the first study that

addresses biodiversity effects in tree hosts-foliar fungal pathogen systems in a full tree-experimental setting.

Methods

Study site

The BIOTREE project adopts a "synthetic community approach" to study tree diversity effects on ecosystem functioning. Study sites were established by experimentally creating a gradient of tree species richness under relatively homogeneous site conditions. The project has been described in detail elsewhere (Scherer-Lorenzen et al. 2007), so that we report the most important design features only. The study site at Kaltenborn was selected from the three BIOTREE sites and is located in South-West Thuringia (50°47′ N, 10°13′ E), Germany. Elevation is about 320–350 m a.s.l., mean annual temperature is 7.8°C and mean annual precipitation is about 650 mm (Scherer-Lorenzen et al. 2007). The climate is subatlantic, the soils are acidic and sandy. In 2003/2004, 16 plots were established that contained either 1 (n = 4), 2 (n = 6), 3 (n = 4) or 4 (n = 2) tree species (*Quercus*, *Fagus sylvatica*, *Picea abies*, *Pseudotsuga menziesii*; Scherer-Lorenzen et al. 2007). Individuals of the genus *Quercus* mainly belonged to the species *Quercus petraea*, but there were also a few individuals of *Quercus robur* and potentially some hybrids of both *Quercus* species planted. The occurrence of this within genus mixture is caused by a less strict differentiation between those *Quercus* species in the tree nurseries as well as by the high hybridization rate between both species. Since these two species are known to be closely related and do not differ much ecologically, we refer to them as *Quercus*. The replicates of the four-species mixture always contain the same species composition, while at all other diversity levels, species composition differs between replicates. The plots have a size of 120 × 48 m and are divided into three subplots which will receive a different management in the future (unmanaged, managed, managed with additional tree species), but are equivalent for the purpose of our study. Each subplot consists of 30 mono-specific patches of 8 × 8 m. Mimicking local forestry practices, patches with *Quercus* and *F. sylvatica* were planted at higher densities, comprising 28 tree individuals, whereas those with *P. abies* and *P. menziesii* have 16 tree individuals. Detailed information about the plot design and tree establishment success at the Kaltenborn site is given in Scherer-Lorenzen et al. (2007) and Don et al. (2007).

Tree individuals were randomly selected for foliar fungal pathogen analyses in every plot, mostly using the unmanaged subplots and excluding all patches at the outer border of a plot to avoid edge effects when calculating local neighborhood composition. The random selection of trees resulted in the selection of both trees growing in the centre and at the edge of each tree species patch. The mean tree size of sampled individuals at the time of sampling in September 2010 varied between 2.4 + 0.4 m for the smallest species (*Quercus*) and 3.5 + 0.7 m for the tallest species (*Pseudotsuga*), respectively. In total, we sampled six individuals in each of the monocultures, three individuals per species in each of the two-species mixture plots and two individuals per species in each of the three and four species mixtures. In total, 100 trees were sampled.

Leaf sampling

On deciduous trees, two branches, growing in opposite directions were selected in the upper as well as in the lower part of the crown and 20 leaves were collected from every branch. On conifers, eight shoots were sampled with needles of both the recent and all previous years. Leaves and needles were dried immediately after sampling at 60°C for three days and then stored in the dark at approximately 20°C.

Macro- and microscopic analyses

For macro- and microscopic analyses we used a random subset of 10 leaves or 100 needles per tree individual of each of the 100 sampled individuals. We included only visible pathogenic foliar fungi in this study, but excluded visible saprophytic and epiphytic fungi, since they have different ecological functions. In addition, one has to be aware that there were also endophytic fungi, which might also have an impact on the host, but were not investigated in this study. Thus, the restriction of fungal species inventory to visible parasitic fungi leads to an exclusion of all other fungi living on the leaf surface as well as within the tissue, resulting in a smaller amount of

fungal species diversity.

Light microscopy was used to identify pathogenic fungal taxa to the species level (after Brandenburger 1985, Ellis and Ellis 1997, Braun and Cook 2012). Depending on the fungal developmental stage identification was not always possible at the species level. In one case we could only assign a taxon without fructification to the phylum level of Ascomycota. Binocular analyses of the collected and dried leaves allowed the quantification of pathogen load of fungal taxa on the whole surface of leaves and needles. Pathogen load was estimated as percent leaf area damage on a percentage scale with categories of 0%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75% and 76–100%.

Data analyses

Both fungal species richness and pathogen load were related to tree species richness/Shannon diversity of the local tree neighborhood and to tree species identity. Local tree neighborhood was calculated from all eight patches around the central patch with the target individual, including also the trees in the central target, and thus comprising 9×16 (n = 144, conifers) to 9×28 (n = 252, deciduous trees) trees. Effects were assessed at three different hierarchical levels. At the community scale, the *plot level*, all tree und fungal species and their pathogen load were jointly analyzed (n = 100 tree individuals), providing insights in overall pathogen diversity and pathogen load with respect to community diversity. Using sequential linear models, in a first model, the effect of tree species richness as main predictor was accounted for. However, that model included a certain part of remaining variance, which might be explainable by further biodiversity effects. Thus, in a second step, the residuals of that model were used for testing species identity effects, using presence/absence coding for the identity of all four tree species in the experiment and following the procedure outlined in Bell et al. (2009). At the local neighborhood scale, fungal species richness and pathogen load data were analyzed separately by tree species at the *tree species level*, taking each of the four tree species as target species (n = 25 tree individuals per tree species). This analysis by tree species separation was done due to differences of host species' susceptibility and species specific host-pathogen interactions. In addition, at the *fungus species level*, pathogen load was evaluated separately for every fungal taxon on a particular tree species (n = 25 tree individuals per tree species), since infectiousness and biology of each fungal taxa were different. We used linear mixed effects models (*lme*, package nlme, Bates 2011) at the *tree species level* and *fungus species level*, including plot as random factor (R Development Core Team 2008), testing for specific effects of Shannon diversity of the local neighborhood and neighbor identity. As in the ordinary linear models, residuals of the model with Shannon diversity as main predictor were tested for species identity effects of all four tree species in a subsequent mixed model. F tests and p values were obtained from the mixed models with the *cftest* command (package multcomp). The variance components analysis (varcomp procedure) was used to assess the proportion of total random variation to be attributed to plot. The amount of variation explained by the model was obtained from regressing predicted against observed responses. All figures were produced with R.

Results

Statistical analysis showed that *Quercus* seemed to be the tree species in the Kaltenborn-Experiment that was most affected, in terms of pathogen load and with four different foliar pathogen species also with respect to number of pathogen species. Two of the pathogens, with the highest frequency of occurrence and quantity of infection, were powdery mildew species (*Erysiphe alphitoides* (Griffon & Maubl.) U. Braun & S. Takam., *Erysiphe hypophylla* (Nevod.) U. Braun & Cunningt.). The other two fungi species occurred only in low frequency and coverage on the leaves, *Microstroma album* (Desm.) Sacc. and an unidentified species of Ascomycota (Berk.) Caval.-Sm. A third powdery mildew species (*Phyllactinia orbiculata* (Ehrenb.) U. Braun) was detected on *Fagus sylvatica*, but this fungus species showed a lower pathogen load than the powdery mildew species on *Quercus*. *Fagus sylvatica* was host of a second foliar pathogen species (*Apiognomonia errabunda* (Roberge ex Desm.) Höhn.). In contrast, foliar pathogens were neither encountered on *Pseudotsuga menziesii* nor

Table 1. Linear model results at the *plot level*. Effect of tree species richness on number of fungus species and pathogen load (%) across all plots (n = 16).

Response variable	df	SS	F	p
No. fungus species	1	14.504	2.784	0.117
Residuals	14	72.933		
Pathogen load (%)	1	57.29	0.499	0.491
Residuals	14	1604.60		

Table 2. Linear model results at the *plot level*. Effect of tree species identity on number of fungus species and pathogen load (%) across all plots (n = 16). Significant results are indicated in bold fonts.

	No. fungus species		Pathogen load (%)	
Identity effect	Estimate	p	Estimate	p
Quercus	3.375	**<0.001**	15.094	**<0.001**
F. sylvatica	0.125	0.563	−5.365	0.053
P. menziesii	−1.875	**<0.001**	−3.813	0.154
P. abies	−1.625	**<0.001**	−5.917	**0.036**

on *Picea abies*.

At the community scale, linear model analysis at the *plot level* showed no significant tree species richness effects, neither on fungal species richness nor on pathogen load (Table 1; Appendix: Fig. A1). However, the presence of *Quercus* within the community positively affected fungal species richness and pathogen load, indicating a higher fungal species richness and pathogen load when *Quercus* was present in a plot. In contrast, *F. sylvatica*, *P. menziesii* and *P. abies* exhibited mostly negative tree species identity effects on both response variables (Table 2).

With a focus on the local neighborhood scale, at the *tree species level*, Shannon diversity of the local tree neighborhood had no significant effects on fungal species richness (Table 3). There was a marginally significant positive effect on pathogen load of *Quercus* while there were no effects on pathogen load of the other tree species (Table 3; Appendix: Fig. A2). In contrast to the *plot level*, no species identity effects were encountered at the *tree species level* (Appendix: Table A1).

Similarly, at the local neighborhood scale at the *fungus species level*, we found that pathogen loads of the two powdery mildew species *Erysiphe alphitoides* and *Erysiphe hypophylla* on *Quercus* were negatively related to Shannon diversity of the local tree neighborhood (Fig. 2a, Table 4). However, there was no effect of tree species neighborhood richness on *Microstroma album* and the unidentified leaf-spotting ascomycet species on *Quercus* (Table 4). Fig. 2b shows for the host *F. sylvatica* that Shannon diversity of local tree neighborhood affected the powdery mildew *Phyllactinia orbiculata*, too, whereas there was no effect on *Apiognomonia errabunda* (Table 4). As for the *tree species level*, no tree species identity effects were detected at the *fungus species level* (Appendix: Tables A2 and A3).

Discussion

Loss of biodiversity might have extensive, positive or negative, impacts on disease transmission in natural ecosystems (Borer et al. 2009, Haas et al. 2011). Our study showed that tree diversity plays a role in biotrophic fungal pathogen infections of common European forestry species. We have to reject the first hypothesis that species number of foliar biotrophic fungi at the *plot level* is positively and pathogen load is

Table 3. Linear mixed model results at the *tree species level*. Effect of Shannon diversity of the local tree neighborhood on number of fungus species and pathogen load (%) for all target trees (n = 100, plot variance = 22.2% and 31.8% of total random variation, respectively) and for the tree species *Quercus* (plot variance = 8.5%) and *Fagus sylvatica* (plot variance = 47.1%) across all tree individuals of each tree species (n = 25). Df of the numerator = 1, df of the denominator = 83 for all target trees and df = 15 for *Quercus* and *F. sylvatica*. Note that no fungal pathogens were detected on *Picea* and *Pseudotsuga*.

		All target trees		*Quercus*		*F. sylvatica*	
Response variable	Predictor variable	F	p	F	p	F	p
No. fungus species	Intercept	23.242	<0.001				
	Shannon diversity	0.047	0.828				
Pathogen load (%)	Intercept	9.07	0.003	58.487	<0.001	7.347	0.016
	Shannon diversity	0.619	0.434	3.209	0.094	2.448	0.139

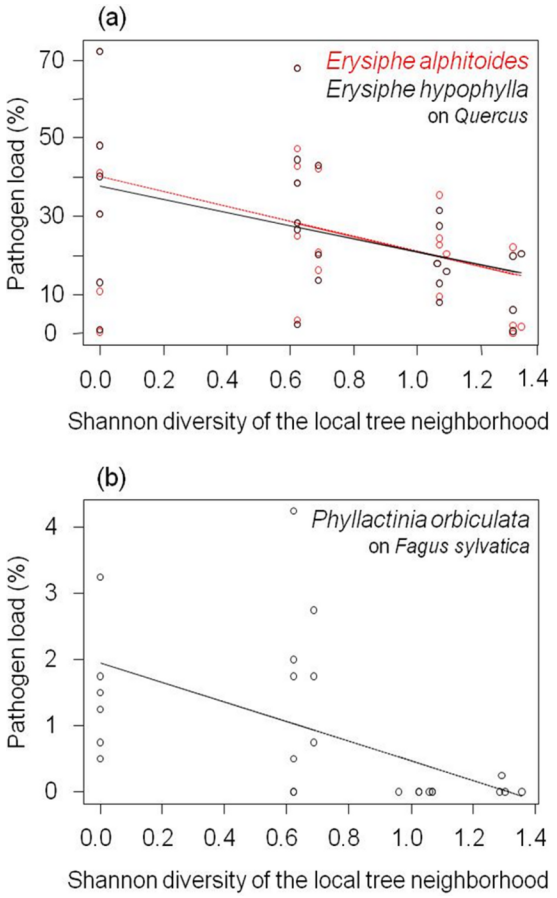

Fig. 2. Relationship between Shannon diversity of the local tree neighborhood and pathogen load of (a) *Erysiphe alphitoides* (red; $R^2 = 0.288$, $p = 0.054$, $n = 25$) and *E. hypophylla* (black; $R^2 = 0.169$, $p = 0.047$, $n = 25$) on *Quercus* and (b) *Phyllactinia orbiculata* on *Fagus sylvatica* ($R^2 = 0.66$, $p = 0.055$, $n = 25$).

negatively related to the number of host tree species. There are several explanations for this outcome at the community scale. First, the number of host tree species might not have been able to affect overall species number and pathogen load of foliar biotrophic fungi, because the two conifer species have not been infected by any fungal pathogen. Thus, at the community scale, there was only a gradient of two competent tree species instead of the four tree species in the whole experiment. The immunity of conifers to foliar biotrophic fungi is a feature observed before and might be brought about by both constitutive and inducible defenses (Erbilgin and Colgan 2012). Second, none of the biotrophic

Table 4. Linear mixed model results at the *fungus species* level. Effect of Shannon diversity of the local tree neighborhood on pathogen load (%) of specialized fungus species for the tree species *Quercus* and *Fagus sylvatica* across all tree individuals of each tree species (n = 25). Df of the numerator = 1, df of the denominator = 15. Significant results are indicated in bold fonts. Plot variance of total random variation: *E. alphitoides* = 8.5%, *E. hypophylla* <0.1%, *M. album* = 3.9%, Species of *Ascomycota* = 28.5%, *P. orbiculata* = 44.0%, *A. errabunda* = 21.5%.

Response variable	F	p
Pathogen load (%) of fungus species on *Quercus*		
Intercept	40.478	<0.001
Erysiphe alphitoides	4.388	**0.054**
Intercept	53.76	<0.001
Erysiphe hypophylla	4.689	**0.047**
Intercept	3.439	0.084
Microstroma album	0.04	0.845
Intercept	6.721	0.020
Species of *Ascomycota*	0.262	0.616
Pathogen load (%) of fungus species on *F. sylvatica*		
Intercept	6.677	0.02
Phyllactinia orbiculata	4.317	**0.055**
Intercept	6.151	0.026
Apiognomonia errabunda	0.044	0.836

fungi in our study were generalist species or depended on multiple hosts. Our results support the idea that host species richness mainly favors generalist pathogens rather than specialized pathogens, which was shown for generalist vs. specialist herbivores (Koricheva et al. 2006). Third, the young age of the tree individuals in the BIOTREE experiment may have retarded potential host richness effects (Scherer-Lorenzen et al. 2007).

As expressed in the second hypothesis, strong tree species identity effects on fungal species attack at the *plot level* were caused by the presence of particular disease-prone tree species. The high host-specifity of foliar biotrophic pathogens is the ecological consequence of the highly specific molecular mechanisms of host-pathogen interactions (Keen 1990, Chisholm et al. 2006). The strong identity effects mainly depended on a positive effect of *Quercus* and a negative one of *Fagus sylvatica*, *Pseudotsuga menziesii* and *Picea abies*. In addition, the susceptibility of *Quercus* to fungal leaf diseases is not easily explained by the species' leaf traits. The leaves of *Q. petraea* as those of *Q. robur* are neither short-lived, nor nutrient rich or poorly defended, as

proposed by the host physiological phenotype hypothesis (Cronin et al. 2010). On the contrary, *Q. petraea* leaves have exceptionally high contents of tannin and non-tannin phenolics (Estiarte et al. 2007; Eichenberg et al., *unpublished manuscript*). Alternatively, the load of host-specific pathogens might be less dependent on the host's traits but on the host species' range sizes and local abundance, as demonstrated by Schuldt et al. (2012) for host-specific herbivory.

In contrast, at the *tree species level* we encountered a negative effect of the tree richness in the local neighborhood on pathogen load of foliar biotrophic fungi, thus supporting the third hypothesis with focus on the local neighborhood scale. This effect was even clearer at the *fungus species level*, where tree richness reduced the pathogen load of several powdery mildew species. Such negative biodiversity effects have been described previously for grasslands (Mitchell et al. 2002, Roscher et al. 2007) and also for crops (Zhu et al. 2005), but not yet for forest communities. The negative tree richness effects on pathogen load of foliar biotrophic fungi probably resulted from a dilution effect with increasing tree species richness, because two trees species carried no pathogens at all, thus including more zeros in the numerator while increasing the denominator.

In contrast to the fourth hypothesis, tree species identity effects were not encountered at the *tree species level* and *fungus species level*. In contrast to the community scale, where species identity effects result from host-specific contributions to the plot's pathogen load and are solely brought about by the presence or absence of disease-prone host tree species, species identity effects at the local neighborhood scale would only operate through a change in environmental conditions, such as microclimate, or through changes in competitive hierarchies. No such effects were encountered in our study. This implies that the dilution effect brought about by tree richness at the local scale does not depend on the characteristics of the trees in the local neighborhood. Thus, solely the density of the target tree seems to be the key factor for fungal pathogen load, while the characteristics of the diluting matrix are unimportant. This clearly points to reduced transmission rates of pathogens as the main cause of the observed dilution effect at the local neighborhood scale (Keesing et al. 2010, Haas et al. 2011).

In conclusion, our study provides clear evidence for biodiversity effects in disease risk and pathogen transmission of specialized biotrophic fungi in temperate forest systems. To our knowledge this is the first time that biodiversity effects were experimentally demonstrated for tree host-foliar fungal pathogen systems on four different tree species. Furthermore, our findings clearly point out the paramount importance of species identity effects at the community scale, while tree species richness effects were only apparent at the local neighborhood scale. This indicates that these two drivers of ecosystem functioning might operate at different spatial scales, which has not been tested so far.

Acknowledgments

We are grateful to Mathias Baudis for helping with the field work. We would like to thank Michael Allen, Ben Sikes and one anonymous referee who gave valuable comment on the draft of the manuscript. A Graduate Scholarship of Saxony-Anhalt and a grant of the Scholarship Programme of the German Federal Environmental Foundation (DBU) are highly acknowledged. The research leading to these results has also received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 265171, project FunDivEUROPE.

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Supplemental Material

Appendix

Table A1. Linear mixed model results at the *tree species* level. Effect of tree species identity of the local neighborhood on number of pathogen species and pathogen load (%) for all target trees (n = 100, plot variance of total random variation 22.2% and 31.8%, respectively) and for the tree species *Quercus* (plot variance = 8.5%) and *Fagus sylvatica* (plot variance = 47.1%) across all tree individuals of each tree species (n = 25).

		No. pathogen species		Pathogen load (%)	
Target species	Identity effect	Estimate	p	Estimate	p
All tree species	*Quercus*	0.484	0.060	3.984	0.108
	F. sylvatica	0.023	0.922	−1.411	0.551
	P. menziesii	−0.3	0.224	−1.006	0.669
	P. abies	−0.207	0.392	−1.552	0.512
Quercus	*F. sylvatica*			−3.425	0.612
	P. menziesii			5.998	0.385
	P. abies			−3.503	0.604
F. sylvatica	*Quercus*			0.033	0.927
	P. menziesii			−0.331	0.371
	P. abies			0.273	0.454

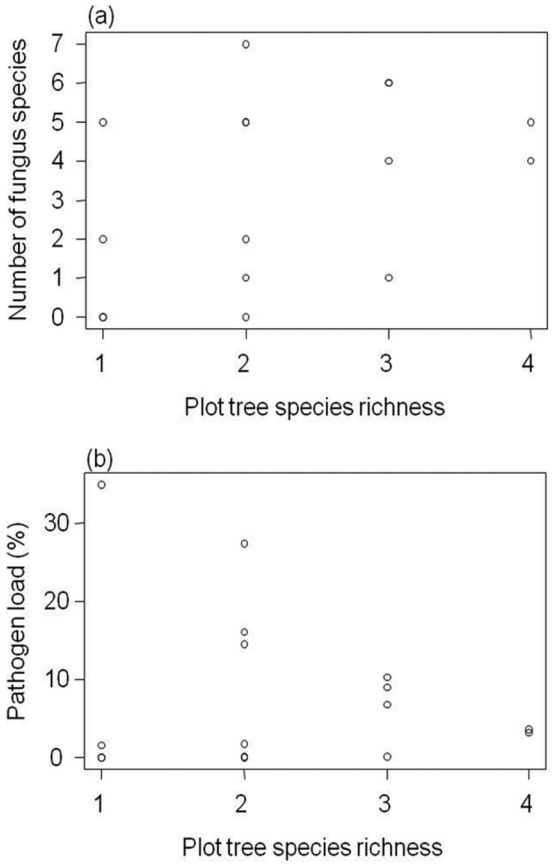

Fig. A1. Relationship between plot tree species richness and (a) the number of fungus species encountered in the whole plot ($R^2 = 0.315$, $p = 0.117$, $n = 16$) and (b) average pathogen load per plot ($R^2 = 0.224$, $p = 0.491$, $n = 16$).

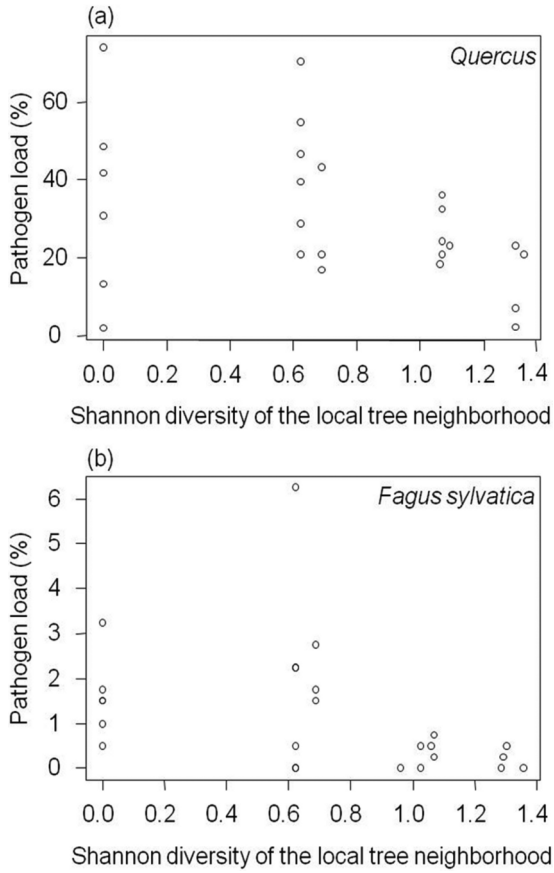

Fig. A2. Relationship between Shannon diversity of the local tree neighborhood and pathogen load on (a) *Quercus* ($R^2 = 0.252$, $p = 0.094$, $n = 25$) and (b) *Fagus sylvatica* ($R^2 = 0.644$, $p = 0.136$, $n = 25$).

Table A2. Linear mixed model results at the fungus species level. Effect of tree species identity of the local neighborhood on pathogen load (%) of specific fungus species for the tree species *Quercus* across all tree individuals of the tree species (n = 25). Plot variance of total random variation: *E. alphitoides* = 8.5%, *E. hypophylla* < 0.1%, *M. album* = 3.9%, Species of *Ascomycota* = 28.5%.

	Erysiphe alphitoides		*Erysiphe hypophylla*		*Microstroma album*		Species of *Ascomycota*	
Identity effect	Estimate	p	Estimate	p	Estimate	p	Estimate	p
F. sylvatica	−2.579	0.714	−2.666	0.708	−0.433	0.624	−0.509	0.289
P. menziesii	5.195	0.468	6.732	0.36	−0.432	0.625	0.174	0.705
P. abies	−3.606	0.61	−4.768	0.509	0.798	0.378	0.29	0.532

Table A3. Linear mixed model results at the fungus species level. Effect of tree species identity of the local neighborhood on pathogen load (%) of specific fungus species for the tree species *Fagus sylvatica* across all tree individuals of the tree species (n = 25). Plot variance of total random variation: *P. orbiculata* = 44.0%, *A. errabunda* = 21.5%.

	Phyllactinia orbiculata		*Apiognomonia errabunda*	
Identity effect	Estimate	p	Estimate	p
Quercus	0.052	0.859	−0.031	0.834
P. menziesii	−0.262	0.382	−0.176	0.261
P. abies	0.195	0.51	0.19	0.229