Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi

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Summary

1. The identification of traits that influence the responses of the species to environmental variation provides a mechanistic perspective on the assembly processes of ecological communities. While much research linking functional ecology with assembly processes has been conducted with animals and plants, the development of predictive or even conceptual frameworks for fungal functional community ecology remains poorly explored. Particularly, little is known about the contribution of traits to the occurrences of fungal species under different environmental conditions.

2. Wood-inhabiting fungi are known to strongly respond to habitat disturbance, and thus provide an interesting case study for investigating to what extent variation in occurrence patterns of fungi can be related to traits. We apply a trait-based joint species distribution model to a data set consisting of fruit-body occurrence data on 321 wood-inhabiting fungal species collected in 22 460 dead wood units from managed and natural forest sites.

3. Our results show that environmental filtering plays a big role on shaping wood-inhabiting fungal communities, as different environments held different communities in terms of species and trait compositions. Most importantly, forest management selected against species with large and long-lived fruit-bodies as well as late decayers, and promoted the occurrences of species with small fruit-bodies and early decayers. A strong phylogenetic signal in the data suggested the existence of also some other functionally important traits than the ones we considered.

4. We found that those species groups that were more prevalent in natural conditions had more associations to other species than species groups that were tolerant to or benefitted from forest management. Therefore, the changes that forest management causes on wood-inhabiting fungal communities influence ecosystem functioning through simplification of interactive associations among the fungal species.

5. *Synthesis.* Our results show that functional traits are linked to the responses of wood-inhabiting fungi to variation in their environment, and thus environmental changes alter ecosystem functions via promoting or reducing species with different fruit-body types. However, further research is needed to identify other functional traits and to provide conclusive evidence for the adaptive nature of the links from traits to occurrence patterns found here.

Key-words: co-occurrence, forestry, functional diversity, habitat fragmentation, morphological trait, phylogenetic signal, reproductive trait, trait composition

Introduction

Functional traits determine the responses of individuals and species to biotic and abiotic variation (Gallagher, Hughes & Leishman 2013) and thus influence the ability of organisms to adapt to particular environmental characteristics (Moretti & Legg 2009). Traits that influence the responses of species to changes in environmental conditions are called response-traits. The identification of response-traits can provide functional, mechanistic and predictive perspectives on processes shaping the assembly and dynamics of ecological communities (Suding *et al.* 2008; Cadotte *et al.* 2015). Thus, analysing

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community composition in terms of functional traits can be more informative than analysing community composition in terms of species identities (McGill *et al.* 2006; Cadotte, Carscadden & Mirotchnick 2011).

Many recent studies have focused on linking functional ecology with assembly processes in fungal community ecology (Crowther *et al.* 2014; Aguilar-Trigueros *et al.* 2015; Treseder & Lennon 2015; Halbwachs, Simmel & Bässler 2016). Previous research on wood-inhabiting fungal communities has suggested that neutral processes have a big role in shaping fungal assemblages, as they involve much random variation, especially at small spatial scales (e.g. Bässler *et al.* 2012; Abrego *et al.* 2014). The most deterministic niche-based processes that have been found to influence the structure of wood-inhabiting fungal communities relate to the responses of the species to the physio-chemical characteristics of the resource units (mainly the sizes and decay stages of the dead wood units), and the intensity of forest land-use (e.g. Hottola, Ovaskainen & Hanski 2009; Nordén *et al.* 2013; Thorn *et al.* 2016). Spore size, spore wall thickness, fruit-body size, habitat specialization level and rarity have been detected as key traits determining the occurrences of fungal species on different resource types and environments with different levels of management intensities (Nordén *et al.* 2013; Bässler *et al.* 2014, 2016; Norros *et al.* 2014, 2015). In particular, wood-inhabiting fungal species with large and robust fruit-bodies have been identified to be vulnerable to forestry practices, most likely due to the removal of large resources that they require (Bässler *et al.* 2014, 2016). The vulnerability of wood-inhabiting fungal species to forest management is also influenced by their rarity and habitat specialization to dead wood characteristics and forest structure (Penttilä, Siitonen & Kuusinen 2004; Berglund *et al.* 2011; Junninen & Komonen 2011; Nordén *et al.* 2013). Spore size has been proposed to be a trait that determines the occurrences of fungal species in fragmented environments, as it is related both to dispersal distance and establishment success (Kauserud *et al.* 2011; Norros *et al.* 2014, 2015). Fragmented habitats have higher amounts of edges, which according to the experimental results of Norros *et al.* (2015) are potentially beneficial environments for species with thick walled spores. Another trait that has been suggested to relate to tolerance to harsh climatic conditions is the structure of the fruit-body (Lindblad 2001; Bässler *et al.* 2010; Halbwachs, Simmel & Bässler 2016). Species with annual, soft and thin fruit-bodies are likely to be more sensitive to climatic fluctuations than species with perennial, hard and thick fruit-bodies (Lindblad 2001; Bässler *et al.* 2010).

In spite of the research reviewed above, only little is known on which traits significantly influence the occurrences of fungi under different environmental conditions, and even less is known about the directions and magnitudes of those influences. Furthermore, it is well documented that species not only do not respond to environmental variation independently of each other but also interspecific interactions play an important role in determining the community-level responses of wood-inhabiting fungi (Hiscox *et al.* 2015; Abrego *et al.* 2016b;

Thorn *et al.* 2016). In spite of this, the distribution of interspecific interactions across traits has not been investigated. Understanding the link between traits and interspecific interactions is critical for gaining ecosystem level insights, such as assessing indirect responses to habitat loss mediated through species interactions, as well as predicting how interspecific interactions are likely to be modified by changes in environmental conditions (Chapin *et al.* 2000; Abrego *et al.* 2016b).

In this study, our aim is to link fungal traits to community assembly processes by examining to what extent variation in occurrence patterns can be related to traits that have been hypothesized to be of functional importance. As is commonly done in plant community ecology (Pérez-Harguindeguy *et al.* 2013), we consider fungal functional traits to be any morphological, physiological or phenological features that can potentially affect the fitness of the fungal species, restricting the analysis to traits for which data were available in the literature. To address this aim, we use an extensive data set on species occurrence that involves major variation in fungal taxonomic groups as well as in environmental characteristics. We apply a trait-based joint species distribution model to relate variation in fruit-body occurrences of wood-inhabiting fungi to environmental characteristics. Specifically, we aim to (i) assess which traits influence the link from environmental conditions (forest management, distance to forest edge and the properties of the resource units) to species occurrence; (ii) measure how much of the responses of the species to their environment can be attributed to traits; (iii) predict how the communities inhabiting different kinds of forest scenarios vary in their trait composition; and (iv) assess whether species-to-species associations are randomly or non-randomly distributed with respect to the species traits.

Materials and methods

STUDY AREA AND DATA COLLECTION

The species occurrence data are the same as used in Abrego & Salcedo (2013, 2014) and published in Abrego *et al.* (2016a). The inventories were conducted in the European beech (*Fagus sylvatica*) distribution area of Navarre (northern Spain) (Fig. 1). In this area, we visited all protected areas where forest management has allowed the conservation of old-growth beech forests, and considered them as the reference 'natural' forest sites. As 'managed' forest sites, we randomly selected beech forest sites which are continuously managed by thinning. For more specific details on how the selection procedure was carried out, see Abrego & Salcedo (2013, 2014). Altogether, 8 natural and 21 managed forest sites were included (Fig. 1). We surveyed in each forest site 5–10 randomly located 10 × 10 m sample plots, in total 230 plots. Each plot was surveyed once, from late September to early November in 2011 and 2012. In each plot all dead wood pieces (called henceforth resource units) larger than 0·2 cm in diameter were checked and the occurrences of all fungi forming macroscopic fruit-bodies were recorded. Data on the diameter, length and decay stage of all resource units were recorded, whether fruit-bodies were found or not. The diameter and length were used to compute the volume of each dead wood unit, and the decay stage was classified to five classes using a modified form of the classification by
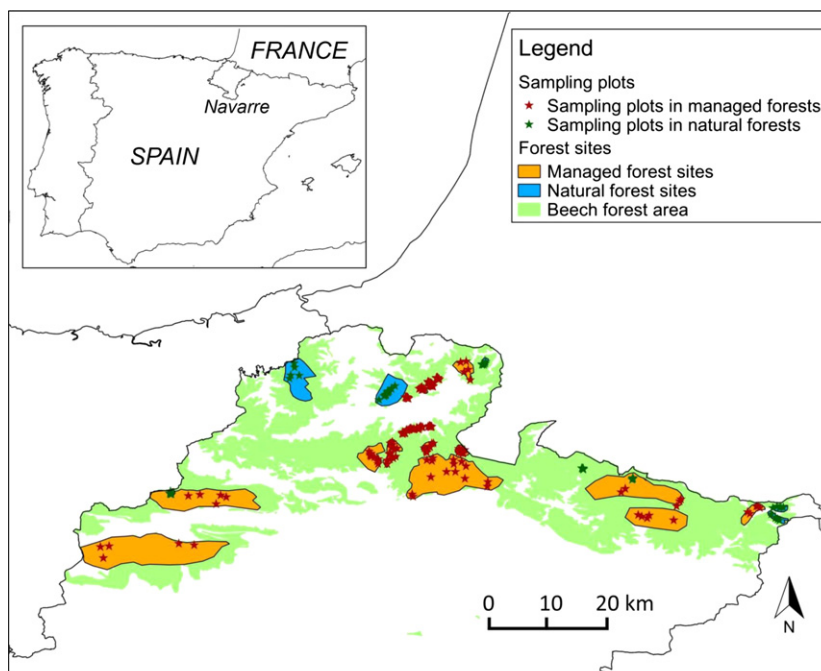
Fig. 1. Map showing the location of the study area and the spatial arrangement of the sampled forest sites and plots. [Colour figure can be viewed at wileyonlinelibrary.com]

Renvall (1995). The distance to the nearest forest edge was measured for each sample plot using aerial photographs in GIS. The data involve 321 species collected from 22 460 resource units, out of which 3809 were located in natural forest sites and 18 651 in managed forest sites. The median, minimum and maximum distances of the plots to the forest edge were 94 m, 4 m and 2534 m respectively.

SELECTED BIOLOGICAL TRAITS

We first compiled data for all traits that we expected to potentially influence the responses of the fungal species to different environmental conditions and for which data were available in the literature. The full set of traits and the consulted references are given in Appendices S1–S3, in the Supporting Information. Altogether, we compiled information about 12 traits, out of which six were related to the structure of the reproductive organs, four to the dispersing propagules and two to the resource use.

We then used principal components analysis (PCA, see Legendre & Legendre 2012) separately for the three different groups of traits (traits related to the reproductive organs, dispersing propagules and resource use) to exclude traits that were highly correlated with other traits. The PCA biplots among the selected and non-selected traits are given in Appendix S4. The selected traits and our *a priori* expectations on how those may relate to the responses of the species to environmental variation is provided in Table 1.

In order to account for the phylogenetic dependencies in the statistical analysis, the species were classified according to the genus, order and phylum, using *Index Fungorum* (http://www.indexfungorum.org/) and *MycoBank* (http://www.mycobank.org/) databases. The taxonomic classifications are given in Appendix S3.

STATISTICAL ANALYSES

Joint species distribution models have recently emerged in the ecological literature as a tool that allows modelling species communities more mechanistically than is possible, for example, with ordination-based approaches (see Warton *et al.* 2015). They allow one to infer from community-level data on species occurrence how species respond to their environment, to relate these responses to traits and phylogenies, and to quantify co-occurrence patterns. We fitted a joint species distribution model to the fungal fruit-body data to simultaneously combine information on traits, environmental covariates, phylogenetic constraints and the spatially hierarchical study design. We then used the parameterized model to quantify how much of the variation in species' responses to environmental variation could be attributed to species traits, as well as to construct predictions on the relationship between environmental conditions and the distribution of traits in the fungal communities.

Description of the fitted statistical model

As our response matrix was the presence–absence of fungal species at the level of resource units, we modelled the data using the Bernoulli distribution and the probit link function. As environmental covariates we included the log-transformed volume, decay class and squared decay class of the resource unit, as well as the log-transformed distance to the forest edge from the sample plot, and the management category (natural or managed) of the forest site. We included random effects (that also model co-occurrence among species) at the levels of resource unit, sampling plot and forest site using a latent factor approach (Ovaskainen *et al.* 2016a). The fitted model includes parameters which measure the influences of the traits on the species-specific responses to the environmental covariates (see Ovaskainen *et al.* 2016b and Appendix S5). The traits that were included in the model are described in Table 1. To account for possible phylogenetic correlations in the species' responses to the environmental covariates, we followed Ives & Helmus (2011), by including a phylogenetic correlation matrix in the model's covariance structure (Appendix S5). In the absence of a quantitative phylogeny, we derived the phylogenetic correlation matrix from the taxonomic tree that included the levels of orders, genera and species, and that assumed an equal branch length for the three levels. The model includes a parameter ρ that measures the strength of the phylogenetic signal in the data, with (i) $\rho = 1$

Table 1. The species traits used in the analyses and their hypothesized relationship with life-history strategy. The categories and units are indicated in the last column

Trait	Hypothesized relationship	Categories or units
Fruit-body type	Due to the amount of biomass and energy needed to form a fruit-body, we expect species with large and robust fruit-bodies (especially pileate polyporoids) to require larger resource units than species with small fruit-bodies (Bässler *et al.* 2014). As large resource units are more common in natural than managed forests, we further expect species with large and robust fruit-bodies to be rare in managed forests. We also expect the species with smaller and less robust fruit-bodies (agaricoids, resupinate corticioids, resupinate polyporoids and tremelloids) to be more sensitive to the climatic conditions from forest edges (Bässler *et al.* 2010; Halbwachs, Simmel & Bässler 2016).	Agaricoid, Resupinate corticoid, Discomycetoid, Pileate corticoid, Pileate polyporoid, Resupinate polyporoid, Ramarioid, Stromatoid, Tremelloid.
Spore size	We expect species with small spores to be more prevalent in managed forests than in natural forests, as small spores disperse further than large spores and thus disperse better in fragmented surroundings (Norros *et al.* 2014). However, we note that large spores have a higher germinability under harsh conditions (Norros *et al.* 2015), leading to the opposite expectation.	Spore volume in μm^3 (log-transformed in the analyses)
Thickness of spore wall	We expect species with thick-walled spores to be more prevalent in forest edges, as species with thick-walled spores are tolerant to UV-light and have a higher germinability under harsh conditions (Norros *et al.* 2015).	Thin, Thick
Presence of ornaments in the spores	Spore ornamentation has been suggested to help on adhering to dispersal vectors (Hussein *et al.* 2013). Hence, species with ornamented spores may be considered as dispersal vector specialists. We expect such species to be more prevalent in natural forests, as in those the dispersal vectors are likely to be more abundant than in managed forests.	Yes, No
Presence of asexual structures in the reproductive layer (cystidia in the case of Basidiomycota and paraphyses in the case of Ascomycota)	Previous studies have shown that the presence of asexual structures in the reproductive layer has, for example, a defensive role against collembolan predation (Nakamori & Suzuki 2007). As such structures make the fruit-body more robust but can be expensive to produce, we expect species that invest to fast growth (resource generalists) to have such structures less often than species that invest to high competitive ability (resource specialists).	Yes, No

indicating that, the residual (after accounting for the effects of the measured traits) environmental responses of the species are fully explained by their phylogenetic correlations, whereas (ii) $\rho = 0$ indicates that the residual environmental responses of the species are randomly distributed with respect to the phylogeny.

We fitted the model to the data with Bayesian inference, using the posterior sampling scheme of Ovaskainen *et al.* (2016a), extended here to account for traits and phylogenetic constraints. The mathematical equations which describe the model structure in full detail are provided in Appendix S5. The prior distributions assumed in the Bayesian analysis are given in Appendix S6.

Variance partitioning

To assess how much of the variation in species occurrences can be explained by traits, we partitioned the total variation in species occurrence in three nested steps. First, we assessed how accurately the model predicted species occurrences at the levels of resource units, plots and forest sites. At the level of resource units, we computed Tjus's R_j^2 (Tjur 2009) for each species. At the plot and forest site levels we computed, for each species, the squared correlations between the predicted and true numbers of occurrences at each plot and forest site respectively. Second, we computed the proportion of the variation on the species' occurrences over the resource units that could be attributed to the measured environmental covariates, compared to that attributed to random variation at the three spatial levels (for technical details, see Appendix S5). Third, we measured how much of the among-species variation to responses to environmental covariates was attributed to traits (for technical details, see Appendix S5).

Scenario simulations

In order to quantify the influence of traits on the responses of species to their environments, we created virtual forests with different resource unit sizes and decay classes (Table 2). Each scenario consists of a 1-ha sample plot. The *Natural forest scenario* was used as the baseline to which the rest of the scenarios were compared to. The *Natural forest scenario* consists of a sample plot located in the interior of a natural forest, and it contains 7500 resource units (the mean number of resource units within natural forests per hectare). The types (sizes and decay classes) of these resource units were randomized by

Table 2. Scenarios used to examine how community structure and trait distribution is influenced by environmental conditions. The Scenario 'Natural' is considered as the baseline, whereas the other scenarios are modifications of the baseline scenario

Scenario	Description
(A) Natural forest	7500 resource units sampled from natural forests. Distance to forest edge 500 m.
(B) Managed forest	18 600 resource units sampled from managed forests. Distance to forest edge 500 m.
(C) Forest edge	As Natural forest, but distance to forest edge 10 m.
(D) Large resource units	As Natural forest, but resource unit diameters changed to 20 cm.
(E) Small resource units	As Natural forest, but resource unit diameters changed to 1 cm.
(F) Early decay class	As Natural forest, but resource unit decay classes changed to 1.
(G) Late decay class	As Natural forest, but resource unit decay classes changed to 5.
(H) Natural forest (different plot)	As Natural forest, but the plot and resource unit random effects were sampled independently.
(I) Natural forest (different forest)	As Natural forest, but the forest, plot and resource unit random effects were sampled independently.

sampling (with replacement) the resource units from those present in the natural forest data. The remaining scenarios are deviations from the baseline scenario. In the *Managed forest scenario*, we assumed that the sample plot is in the interior of a managed forest, and that it contains 18 600 resource units (the mean number of resource units for managed forests per hectare), the types of which were randomized from the managed forest data. The proportion of resource units equal or larger than 10 cm in diameter was 0·03% in managed forests, and 23% in natural forests. The proportion of resource units in early (1–2) and late (4–5) decay stages was 92% and 0·01% in managed forests, and 78% and 5% in natural forests. Thus, the *Natural forest scenario* has a smaller number of resource units but had larger and more decayed resource units than the *Managed forest scenario*. In the *Forest edge scenario*, the sample plot is located at edge of a natural forest. In the *Large resource units scenario,* all resource units were assumed to have 20 cm diameter and 200 cm length (median length for dead wood pieces of that diameter), whereas in the *Small resource units scenario*, all resource units were assumed to have 1 cm diameter and 50 cm length (median length for dead wood pieces of that diameter). In the *Early decay class scenario and* the *Late decay class scenario*, all resource units were assumed to be in the first (1) or last (5) decay class respectively.

We used the parameterized model to generate simulated communities for each of the scenarios described above. To compare the differences among the scenarios to random variation within a scenario, we included two additional scenarios, which were otherwise identical to the baseline scenario of natural forest, but they presented another plot in the same forest, or another plot in a different forest (Table 2). To generate these scenarios, we sampled the random effects of the resource units, plot and forest site (for the scenario representing another forest) independently from those of the baseline scenario. The mathematical details of how the predicted communities were generated are found in Appendix S5.

To characterize the distribution of traits in the simulated communities, we counted the number of occurrences for each species. We then computed the mean spore size over the occurrences, the proportion of occurrences belonging to each fruit-body type, as well as the proportion of occurrences with thick cell wall, ornamented spores or asexual structures in the reproductive layer. We averaged the results over 100 replicates of the simulated communities, each generated with resampled parameters from the posterior distribution.

To summarize how similar the scenarios were in terms of their species identities, we computed the Bray–Curtis dissimilarity index (Bray & Curtis 1957) for all pairs of scenarios from square root transformed data. To illustrate how similar the scenarios were in terms of their trait values, we used the species-specific traits to convert the data of species identities to data on trait compositions. We compared the similarity between trait compositions by calculating the Rao quadratic entropy coefficient (RaoQ) (Rao 1982), which describes the convergence or divergence of traits, in comparison to what would be expected by random (Ricotta & Moretti 2011). We note that while the RaoQ gives information about the convergence or divergence of traits, the prediction of the distribution of traits described above gives information about mean trait values within communities. The RaoQ coefficients were calculated in the R software, using the package 'FD' (Laliberté, Legendre & Shipley 2014). We averaged the Bray–Curtis dissimilarity indices and the RaoQ values over the 100 replicates of the simulated communities, and then performed Principal Coordinates Analysis (PCoA) using the 'vegan' package in the R software (Oksanen *et al.* 2015).

Species-to-species associations

To examine how traits relate to species-to-species associations, we identified species pairs that were linked in the sense that their residual covariance (after accounting for the species' responses to measured environmental covariates) was positive or negative with at least 95% posterior probability, using the same approach as in Ovaskainen *et al.* (2016a). We then examined if the number of links that each species had to the other species was non-randomly distributed across the traits. To do so, we fitted Poisson regression models separately for each of the traits listed in Table 1, where the dependent variable was the number of linked species, and the explanatory variables were the trait categories (for categorical traits) or the trait value (for continuous traits). We performed this analysis in two ways, where we either accounted for or did not account for species abundances by including log-transformed abundance as a predictor. The reason for controlling for abundance is twofold: the actual number of links may be correlated with abundance, in addition to which the statistical power to identify associations among the species is likely to increase with abundance.

Results

HOW DO TRAITS INFLUENCE SPECIES' OCCURRENCE?

Among the traits that were included in the model, only fruit-body type strongly influenced the occurrences of fungal species, with three results gaining statistical support with at least 95% posterior probability (Appendix S7). First, the occurrence probabilities of species in all fruit-body type groups, and in particular in agaricoids, increased with increasing the size of the resource unit. Second, the occurrence probabilities of species in all fruit-body type groups, and in particular in pileate polyporoids, peaked at an intermediate decay class, in the sense of the response to squared decay class being negative.

Third, pileate polyporoids responded more negatively to forest management than species with other fruit-body types.

After accounting for the influences of the measured traits, the phylogenetic signal of the species' responses to environmental variation was very high, the posterior mean (95% credible interval) of the parameter ρ being 0·97 (0·89, 1·00). This suggests the existence of some functionally important trait that are correlated with the phylogeny, but that were not included in our analyses. It further suggests that the taxonomy-based approach used here was a sufficiently good approximation of the true phylogenetic correlations. The models where phylogenetic constraints were or were not controlled for were generally in good agreement, differing only in which groups responded most strongly to the sizes and decay classes of the resource units (Appendix S7).

PARTITIONING VARIATION IN SPECIES OCCURRENCE INTO DIFFERENT COMPONENTS

The explanatory power of the models increased with increasing spatial scale: averaged over the species, the models explained 1%, 5% and 16% of the variation in species occurrence at resource unit, plot and forest site respectively (the species-specific R^2 values are provided in Appendix S8). Out of the explained variance, the fixed effects explained 56%, of which 79% was attributed to the resource unit level covariates (size and decay stage of the resource units), 8% to the plot level covariates (distance from the forest edge) and 13% to the forest site-level covariates (forest management type). The resource unit, plot and forest site-level random effects explained, respectively, 12%, 14% and 18% of the explained variance (Fig. 2). The amount of variation in the species' responses to the environmental covariates that was explained by the measured traits was $R^2_T = 17\%$.

PREDICTING TRAIT COMPOSITION UNDER DIFFERENT SCENARIOS

The communities of macroscopic wood-inhabiting fungi in natural beech forests were dominated by species with resupinate corticioid and stromatoid fruit-body types, followed by species with resupinate polyporoid, pileate polyporoid, agaricoid, pileate corticioid, discomycetoid, ramarioid and tremelloid fruit-bodies (Fig. 3). The mean spore volume (weighted by species occurrences) in natural forests was 42·5 μm^3. Only 10% of the species represented species with ornamented spores, and only 5% represented species with thick walled spores, whereas more than half (60%) of them represented species with asexual structures in the reproductive layer.

Compared to baseline scenario of a natural forest interior, the species richness of wood-inhabiting fungi (*n* values in Fig. 3) was lower in managed forests, at forest edges, and in scenarios where all the resource units were assumed to be small or belong to early or to late decay classes. The highest richness of fungi was obtained under the large resource unit scenario. In contrast to the results on species richness, species abundances (*m* values in Fig. 3) were higher in managed forests than natural forests, likely explained by the fact that managed forests had more resource units (Table 2). The abundances of fungi were especially high in scenarios where the resource units were large or in a late decay stage, and especially low when they were small.

Species with stromatoid fruit-bodies were more abundant in managed forests than in natural forests, whereas species with polyporoid (both resupinate and pileate), pileate corticioid and ramarioid fruit-bodies showed the opposite pattern. Pileate polyporoids were also rarer on small resource units than in the baseline scenario. Resource units in early decay stages were characterized by the abundance of stromatoid species, and the rarity of resupinate polyporoid, resupinate corticioid and ramarioid species. Strongly decayed resource units held very different communities in terms of the fruit-body types compared to the other scenarios, with an excess of resupinate corticioid and ramarioid species, and the rarity of pileate corticioids, pileate polyporoids, stromatoids and tremelloids.

The mean spore size did not differ markedly from that of the baseline scenario for any of the scenarios. We, however, note that it was largest for communities inhabiting large resource units and smallest for communities inhabiting much
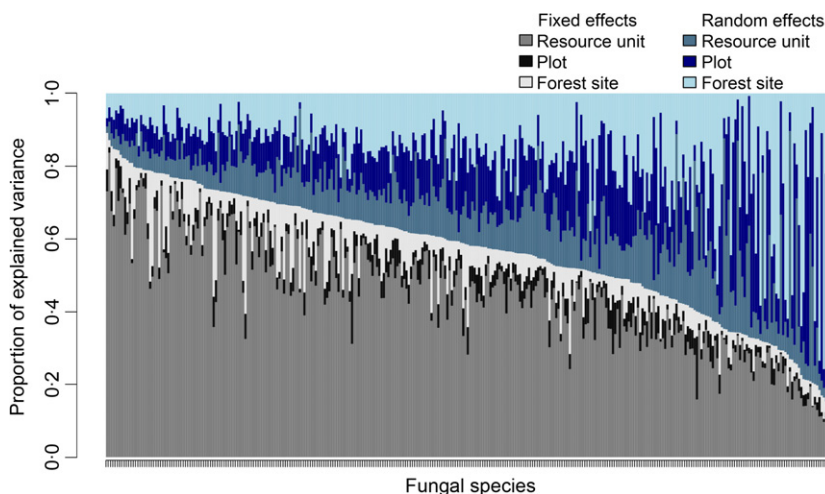

Fig. 2. The relative proportions of variance in species occurrence attributed to the fixed effects and to the random effects at the three spatial scales. The variance attributed to the fixed effects (measured covariates) is shown by dark grey (resource unit level), black (plot level) and light grey (forest site level), whereas the random effects are shown by light blue (resource unit level), dark blue (plot level) and cyan (forest level). The species have been ordered according to the proportion of variance attributed to the measured environmental variables. [Colour figure can be viewed at wileyonlinelibrary.com]
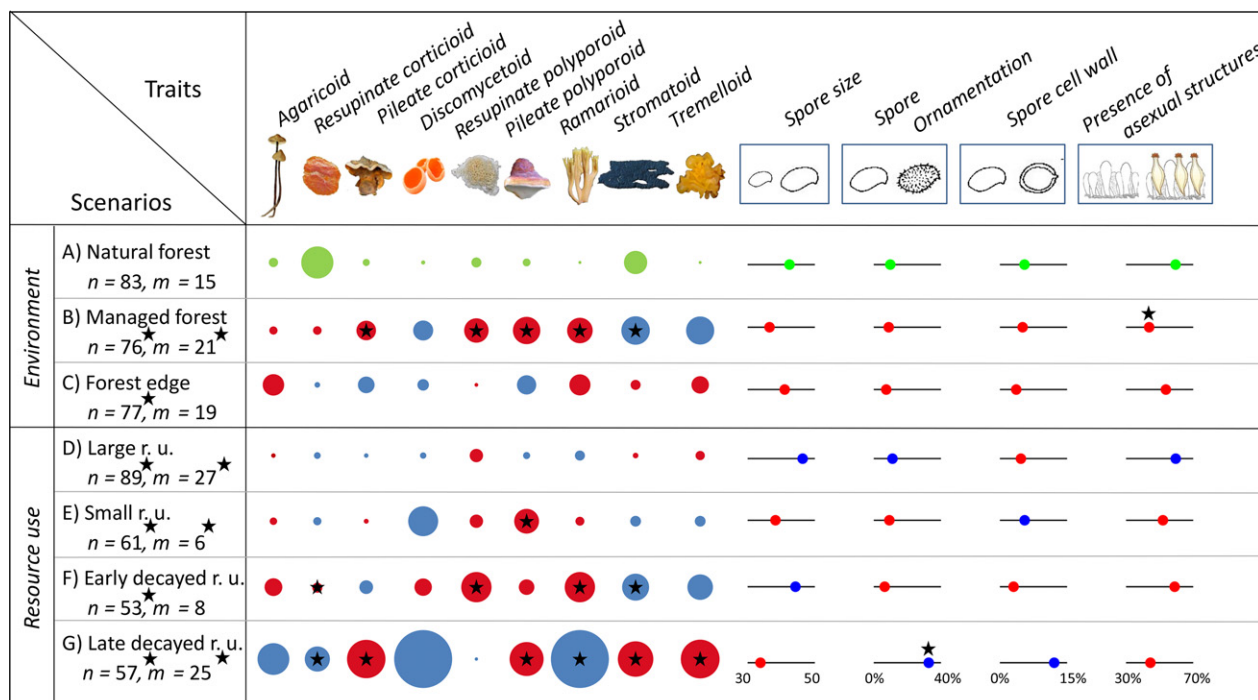
Fig. 3. Distributions of fungal traits in communities inhabiting different kinds of forest environments. The figure is based on the average of 100 communities simulated under the Scenarios listed in Table 2. The numbers *n* and *m* show, respectively, the predicted species richness and the number of occurrences per species, the latter averaged over the species that were present. For the *Natural forest scenario*, the sizes of the green circles show the proportion of occurrences belonging to each fruit-body type. For the other scenarios, the sizes of the dots show how much more common (blue colour) or less common (red colour) the given fruit-body type is relative to the natural forests. For the other traits than fruit-body type, the location of the dot indicates the mean spore size, the proportion of occurrences with ornamented spores, the proportion of occurrences with thick walled spores, and the proportion of occurrences with asexual structures in the reproductive layer. The cases which differ from the baseline scenario of natural forests with at least 95% posterior probability are indicated with a star. For the same data in numerical format, see Appendix S9. [Colour figure can be viewed at wileyonlinelibrary.com]

decayed resource units, these two cases being different from each other with >95% posterior probability. The proportion of ornamented spores was higher for species communities inhabiting resource units in late decay stages than in the baseline scenario. The late decay stage scenario had also the highest proportion of spores with thick cell wall, but the difference to the baseline scenario did not gain strong statistical support. Species with asexual structures in the reproductive layer were rarer in managed forests than in natural forests. The trait proportions estimated from the model where the phylogenetic constraints were not controlled for were very similar to the ones were the phylogenetic constraints were controlled for (Appendix S9).

The similarities among fungal communities under different scenarios were qualitatively similar whether they were measured by species composition or by trait composition (Fig. 4). In both cases, the first axes of the PCoA ordinations related mainly to the effect of the decay stage of the resource unit, which result is consistent with the fact that the forests with resource units in late decay stages held the most dissimilar communities compared to the rest of scenarios (Fig. 3). The second axes of the PCoA related mainly to the effect of the size of the resource unit. Forest sites close to edges were close to natural forests in terms of species composition, whereas in terms of trait compositions they resembled more managed forests and forests with resource units in early decay

stages. Random variation played only a very small role at the level of the 1 ha plots, as the replicated sample plots in the same or different forests were very similar to those of the baseline communities. The PCoA analyses with simulated data generated from the model where phylogenetic constraints were not controlled for (Appendix S10) yielded very similar results to those where phylogenetic constraints were controlled for (Fig. 4).

THE INFLUENCE OF TRAITS ON THE NUMBER OF SPECIES-TO-SPECIES ASSOCIATIONS

After controlling for the effect of species abundance, agaricoids, pileate polyporoids, ramarioids and tremelloids had more links to other species than expected by random, whereas discomycetoids, resupinate polyporoids, and stromatoids had fewer links than expected by random (Fig. 5 and Appendix S11). Furthermore, the number of links increased with spore volume, it was higher for species with thick-walled spores than thin-walled spores, and for species with asexual structures in the reproductive layer (Appendix S11).

Discussion

Our study takes two important steps forward towards a trait-based understanding of the responses of wood-inhabiting

(a) **Principal coordinates analysis for Bray−Curtis**
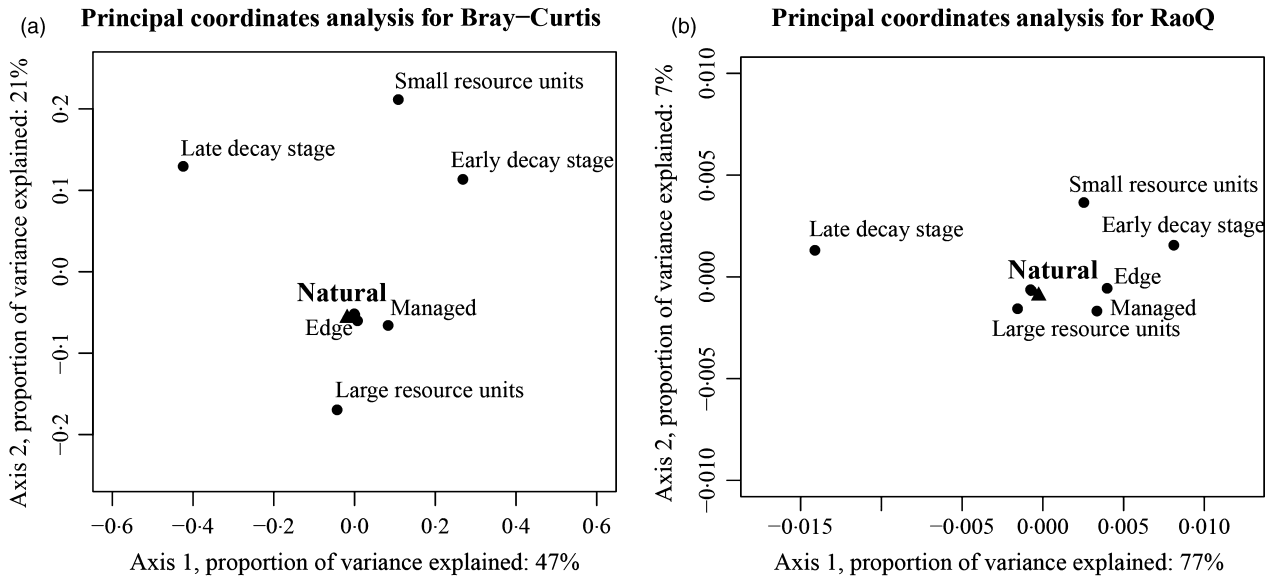
(b) **Principal coordinates analysis for RaoQ**

Fig. 4. Principal coordinates analysis (PCoA) of species communities predicted from the model with phylogeny, for the scenarios A–I listed in Table 2, based on their species (a) and trait (b) compositions. The species composition is measured by the Bray–Curtis dissimilarity index in (a), and the trait composition is measured by the Rao quadratic entropy coefficients (RaoQ) in (b). The baseline Scenario Natural is shown by large bold font, and the natural forests at different plot or at different site are indicated by triangles.
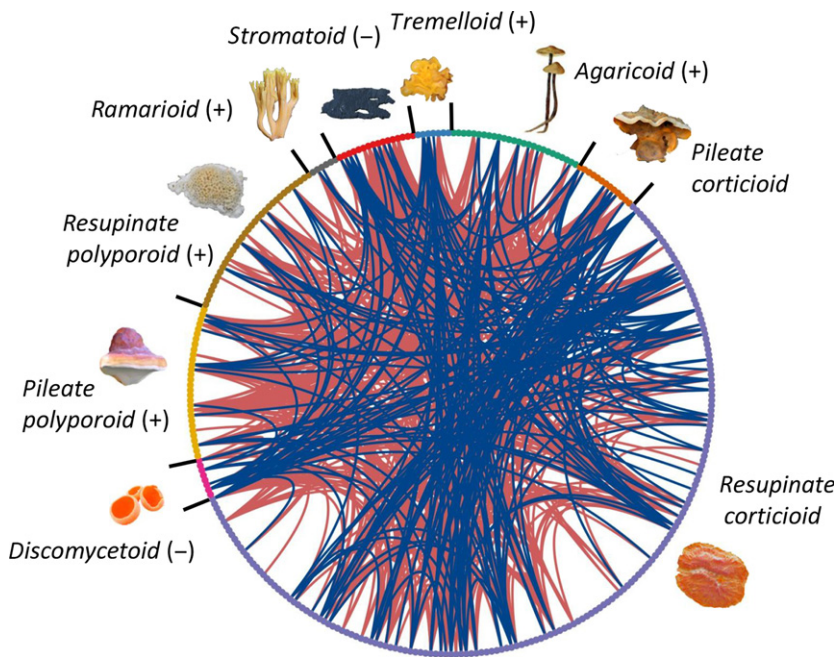

Fig. 5. The distribution of species-to-species associations among different fruit-body types. The species are shown by the dots in the circle, and species pairs are linked by red (respectively, blue) line if they showed a positive (respectively, negative) association with at least 95% posterior probability. In order to visualize the number of links per species with different fruit-body types, species were sorted according to the fruit-body categories. The fruit-body types that showed more (respectively, less) links than expected by random (after controlling for species abundances, see Statistical Analyses) are indicated by a plus sign (respectively, a minus sign). [Colour figure can be viewed at wileyonlinelibrary.com]

fungal communities to environmental variation. Firstly, our results show that forest management acts as an environmental filter which selects species with different fruit-body types, which differ in their life-span, size and robustness, and which are specialized to dead wood of different sizes and decay stages. Secondly, as an important novelty in relation to previous works, our results show that the community-level modification of trait composition driven by forest management simplifies fungal interaction networks.

We found forest management to reduce species richness and to change community structure by reducing the occurrences of

fungi with large, robust and long-lived fruit-bodies as well as late decayers, and by promoting the occurrences of species with small fruit-bodies and early decayers. We, however, recall that our results do not concern all wood-inhabiting fungi, but those forming macroscopic fruit-bodies. Forest management favoured pioneer species with stromatoid fruit-bodies which are typically species with small fruit-bodies, and declined the occurrences of species with pileate corticioid and polyporoid fruit-bodies which include species characterized by large and long-lived fruit-bodies, and ramarioid and resupinate polyporoid species, which occur in the last successional phases of

dead wood decay. Polyporoid species are known to be highly specialist for the habitat type and vulnerable to human-induced habitat disturbances (Junninen & Komonen 2011; Nordén *et al.* 2013). Our results confirmed that compared to other groups of wood-inhabiting fungi, polyporoid fungi with robust and long-lived fruit-bodies are indeed highly vulnerable to forestry practices and specialist for large resources and dead wood in intermediate decay stages. Additionally, our results showed that many other groups of wood-inhabiting fungi are also negatively affected by the effects of forestry practices, especially those occurring in the late successional stages of the dead wood decay (ramarioid and resupinate polyporoid fungi), and those developing robust fruit-bodies (pileate corticioids). Bässler *et al.* (2014) suggested that forest management acts as an environmental filter which decreases the sizes of the fruit-bodies, partly explained by the fact that the size of the available resource units are also smaller (see Küffer & Senn-Irlet 2005; Abrego & Salcedo 2013). Our results show that such a decrease in the fruit-body sizes is related to a gain of small stromatoids in managed forests and especially a loss of pileate polyporoids. Another result for which we gained strong statistical support was that the proportion of species with defensive structures in the reproductive layer was lower in managed forests than in natural forests. This is in concordance with the competition-colonization trade-off theory (Nee & May 1992; Seifan *et al.* 2013), which proposes that in degraded habitats the prevalence of species with poor competitive abilities increases compared to those from undisturbed habitats.

The morphological classification of the fruit-bodies can be paralleled to some well-known functional trait categories in plants (Pérez-Harguindeguy *et al.* 2013). Major classifications of plant traits which can be compared to the fruit-body type of fungi include life-form (*sensu* Raunkiær 1934), growth-form (i.e. the direction and extent of growth) and plant height (Pérez-Harguindeguy *et al.* 2013). Our results showed that fungal species with the longest fruit-body life span, the largest fruit-bodies and the most robust fruit-bodies (i.e. pileate polyporoids) respond most strongly to the effects of forest management, likely because they require large dead wood units to fruit. In an analogous way, in plants, maximum life span is related to tolerance to land use intensification, partly because plants with longer life span are larger in size and thus have a higher nutrient demands, as well as lower dispersal capabilities (Fischer & Stöcklin 1997; Poschlod *et al.* 1998).

In contrast to research in plants (e.g. Fischer & Stöcklin 1997), we did not find evidence for species with large and long-lived fruit-bodies (i.e. pileate polyporoids) to have worse dispersal capabilities (in the sense of having larger spores, see Norros *et al.* 2014) than the rest of species. Furthermore, based on results from plant communities (e.g. Tremlová & Münzbergová 2007; Lindborg *et al.* 2012), we expected fungi from managed forest sites to have smaller spore sizes and thus better dispersal capabilities (Norros *et al.* 2014), but we did not detect strong differences between the mean spore sizes of managed and natural forests sites. In line with our results, no empirical study has found spore size as a critical trait limiting fungal occurrences in managed and fragmented

forests (Nordén *et al.* 2013; Bässler *et al.* 2014). This might be because the dispersal propagules of fungi are much smaller than those of plants (fungal spores are typically less than 10 μm, whereas plant seeds generally exceed one mm and pollen particles are typically over 10 μm) and are thus not so critical in determining their dispersing distances. Future studies covering global spatial scales should confirm whether spore size and its morphology truly influence the responses of fungi to habitat fragmentation and discontinuity.

Our results provide support for the idea that species with annual, soft and thin fruit-bodies are more sensitive to climatic fluctuations than species with long-lived, robust and large fruit-bodies. The communities from forest edges where the climatic fluctuations are more pronounced (see, for example, Crockatt & Bebber 2015), had more species with robust fruit-bodies (pileate fruit-bodies with dimitic hyphae systems) than communities in forest interiors. Similarly, our results provide support to the conclusions of Norros *et al.* (2015) who based on an experimental work, proposed that species with large and thick walled spores are better adapted to persist under the harsh climatic conditions from forest edges: our results suggested that the mean spore size in forest edge is somewhat larger than in forest interior, although we did not get strong statistical support for this result. A possible reason why we failed to record a strong response might be that in our data the edges were not contrasting enough, and/or due to the small spatial scale of our study. Still, our results bring a trait-based perspective to previous studies examining how the responses of the fungal communities to forest edges vary across the wood-inhabiting species (Siitonen, Lehtinen & Siitonen 2005; Caruso, Rudolphi & Rydin 2011; Abrego & Salcedo 2014). Additionally, our results are in line with Crockatt & Bebber (2015) who showed that the decomposition rate of wood in forest edges is lowered, as our results show that the communities from forest edges resemble the communities found on dead wood in early decay stages. Therefore, the morphological classification of the fruit-bodies that we have used in this paper may also be used to measure the climatic resistance of the fungal species.

In terms of the trait composition, we found dead wood in advanced decay stages to harbour the most different communities from the rest of scenarios. Dead wood is strongly modified during the decomposition process both chemically and physically (Harmon *et al.* 1986), which explains why decay stages hold distinct fungal communities (Ottosson *et al.* 2014). In late decay stages dead wood turns into soil, and thus other trophic groups than wood decomposers appear, such as mycorrhizal fungi (Rajala *et al.* 2015). Apart from belonging to another trophic level than wood-decaying fungi, mycorrhizal wood-inhabiting fungi have distinct morphological traits, such as ornamented spores (Halbwachs, Brandl & Bässler 2015), which were in our results especially prevalent in late decayed resource units.

We found some of the species groups that respond negatively to forest management have more associations to other species than by random (pileate polyporoids and ramarioids), whereas those that positively responded to forest management

have less associations to other species than by random (stromatoids). Therefore, our results suggest that the changes that forest management causes on wood-inhabiting fungal communities are likely to influence ecosystem functioning through simplifying the interactive associations among the fungal species. Interactions among fungal species determine the succession pathways of the fungal communities during the dead wood decomposition process (Ottosson *et al.* 2014; Hiscox *et al.* 2015) and ultimately ecosystem functioning (Fukami *et al.* 2010; Dickie *et al.* 2012).

Our results coincide with previous results in suggesting that random processes dominate shaping macroscopic wood-inhabiting fungal communities at small spatial scales (Bässler *et al.* 2012; Abrego *et al.* 2014). One of the reasons why we found such a high amount of random variation is that we carried out a single fruit-body survey, which increased the proportion of rare species in the data set and thus decreased predictability. A molecular detection of the fungal species present at mycelial level would have considerably increased the occurrences of fungal species in the data set (Allmér *et al.* 2006; Kubartová *et al.* 2012). Many species present as mycelia are known to not fruit at all or fruit with a long time delay (Ovaskainen *et al.* 2013). Thus, while a fruit-body-based survey gives direct information on how traits influence the breeding populations of fungi, a molecular approach would have provided complementary information about many other fungal groups which have remained undetected in our study (Ottosson *et al.* 2015), and colonization-establishment processes happening at mycelial level. Furthermore, molecular approaches would enable also measuring additional functional traits, such as those related to colonization capability, mycelial size or the time-delay from mycelial colonization to fruit-body production (Ovaskainen *et al.* 2013). However, conducting molecular surveys for tens of thousands of sampling units would not have been feasible in our study, and thus we hope further studies to overcome this challenge. A fruit-body based survey allowed us to include a very high amount of replicates (i.e. resource units), which decreases the amount of noise in deriving ecological inferences from these kind of data (Abrego *et al.* 2016c). Indeed, while the predictabilities of fungal occurrences at resource units were low, we found predictable patterns to emerge at larger scales that are relevant in terms of representing local communities.

Given the high phylogenetic signal on the responses of the fungal species to the environmental variation, further research is needed to identify other functional traits than those considered here and that have been traditionally considered by fungal ecologists. In order to advance on building a trait-based conceptual framework for fungal community ecology, determining such traits remains as a crucial challenge.

Authors' contributions

N.A. conceived the original idea and collected the data; O.O. developed the statistical methodology and A.N. analysed the data; N.A. wrote the first draft of the manuscript, with specific contributions from O.O. and A.N. All authors commented and edited the subsequent drafts of the manuscript and gave final approval for publication.

Data accessibility

The data used in the case study are available at http://dx.doi.org/10.5061/dryad. 48636 (Abrego *et al.* 2016a) and the Supporting Information.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Table summarizing the traits measured from the literature and their respective categories.

Appendix S2. Literature consulted for the traits of the fungal species.

Appendix S3. List of species and their respective measured traits and taxonomical levels.

Appendix S4. Results from the PCA biplots.

Appendix S5. Detailed explanations on the performed statistical analyses.

Appendix S6. Prior distributions assumed in the statistical analyses.

Appendix S7. 95% credible intervals for the parameters measuring the influence of species traits to environmental responses, for models where the phylogenetic constraints were controlled and not controlled for.

Appendix S8. Species-specific R^2 values measuring model fit at the levels of resource units, plots and forest sites.

Appendix S9. Numerical values for the distributions of fungal traits in communities inhabiting different kinds of forest environments.

Appendix S10. Principal coordinates analysis (PCoA) of species communities predicted from the model without phylogeny.

Appendix S11. Outputs of the Poisson regression models for the number of species-to-species associations depending on traits and species' abundances.