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Species richness of polypores can be increased by supplementing dead wood resource into a boreal forest landscape

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ABSTRACT

1. To prevent local species extinction and to counteract population declines, we must ensure species have access to resources they require for life. This can be done through ecological restoration where previously depleted resources are reintroduced. If the restoration is conducted as a one-off action in a large area, it resembles a natural resource pulse, which should lead to increased abundance of individuals, accompanied possibly by increased species richness. Species-energy relationship and underlying theory enable predictions about how different features of resource pulses affect species richness.
2. We conducted a large-scale, controlled, randomized and replicated field experiment to study the effect of a resource addition on polypore species richness in a previously managed boreal forest landscape in Finland. We manipulated the amount and distribution of dead wood and studied the effects on polypore assemblages on added and natural dead wood during nine years after manipulation (2004-2012).
3. By adding dead wood, species richness grew, mainly through increasing abundances: a large amount of dead wood resulted in higher abundance, higher number and faster accumulation of species than a small amount of dead wood.
4. For a given abundance, dead wood addition contained fewer species than natural dead wood. This is most probably because added dead wood was of low diversity and provided habitat only for a limited number of species.
5. Species richness on natural dead wood increased substantially during the study period, and this increase was not related to the resource manipulation. Thus, habitat improvement through natural succession can occur within a relatively short time period irrespective of human intervention.

6. S*ynthesis and applications.* We demonstrate how the introduction of dead wood additions can strengthen polypore populations. The species taking advance of the introduced resource were primarily common species, instead of rare or red-listed species. Thus, we recommend ensuring the natural formation of dead wood while the populations of the common species supporting ecosystem functions can be increased by adding dead wood in the landscape.

Keywords: boreal forest; dead wood; experiment; resource; restoration; species-energy theory; wood-decaying fungi, polypore species

INTRODUCTION

Human actions have resulted in the depletion of many critical resources that species depend on. To prevent local extinctions and to counteract population declines it is necessary to increase these resources. In boreal forests, intensive forest management has resulted in a significant decrease of the amount of dead wood (Siitonen, 2001). A substantial number of species are dependent on dead wood (Boddy, Frankland, & van West, 2008; Grove, 2002; Heilmann-Clausen, Aude, & Christensen, 2005; Spribille, Thor, Bunnell, Goward, & Björk, 2008), and a large proportion of these species are currently on the verge of extinction (Grove, 2002; Rassi, Hyvärinen, Juslén, & Mannerkoski, 2010). Therefore, the dead wood dynamics in northern forest ecosystems should be restored (Halme et al., 2013). This restoration could be jump-started by dead wood addition, which equals a resource pulse for dead wood dependent species.

Resource pulses are events which provide an increase of resource availability in a fashion which is larger in magnitude and lower in frequency than what is normal for the ecosystem (Yang, Bastow, Spence, & Wright, 2008). Resource pulses generally lead to an increased number of individuals (Yang et al., 2010) and sometimes increased species richness (Drever, Goheen, & Martin, 2009). While a higher number of individuals may provide a link between resource pulse and increased species richness (Drever et al. 2009), the mechanisms of how resource pulses affect species richness require further attention.

The term ‘resource’ have been used almost interchangeably with energy (e.g. Wright, 1983), i.e. energy available for organisms to convert into biomass (*sensu* Evans et al., 2005). It has been widely observed that species richness increases as a function of energy (Field et al., 2009; Hutchinson, 1959; Mittelbach et al., 2001; Waide et al., 1999; Wright, 1983), but only two of the several possible mechanisms behind the species-energy relationship predict that higher energy availability allows for more species via increased number of individuals (Evans, Warren, & Gaston, 2005; Honkanen, Roberge, Rajasärkkä, & Mönkkönen, 2010).

According to the more-individuals hypothesis (Srivastava & Lawton, 1998; Storch, Bohdalková, & Okie, 2018) increased number of individuals allows for a greater number of species with viable population sizes (Evans, Jackson, Greenwood, & Gaston, 2006; Yee & Juliano, 2007). Alternatively, an increased number of individuals results in higher species richness because of random sampling. The more individuals are sampled, the greater the number of species represented of the regional species pool (Evans et al., 2005; Hubbell, 2001; Hurlbert, 2004). Although various studies show positive correlations between energy, the number of individuals and species richness (Storch et al., 2018), it seems that in addition to the number of individuals, also other factors are required for explaining species-energy relationship (Hurlbert, 2004). One possible factor is habitat heterogeneity (Hurlbert, 2004), which can increase in concert with energy, resulting in increased species richness (Abrams, 1995).

In summary, it is unclear whether and why resource pulses lead to increased species richness. Here we explore the effects of an extensive dead wood addition (i.e. resource pulse) on polypore communities within a resource depleted boreal forest landscape. Polypores (bracket fungi) are wood-decaying fungi with immobile fruiting bodies. Thus, their occurrence can be linked reliably to a particular dead wood unit. In a replicated, randomized and controlled experiment, we manipulated the amount and spatial distribution of dead wood and studied the polypore species occurrence over a nine-year period after the resource manipulation. Our hypotheses were: i) dead wood addition increases polypore species richness through increasing their abundance; ii) a large amount of added dead wood results in higher abundance, and thereby in higher species richness and faster colonization of species than a small amount; iii) the relationship between species richness and abundance is independent of the amount of added dead wood; and iv) the aggregated distribution of dead wood results in higher species richness, steeper species-abundance relationship and faster colonization of species than the even distribution of dead wood, provided that the former represents a more heterogeneous resource than the latter.

MATERIALS & METHODS

Study setting

The experiment was established together with the Parks and Wildlife Finland as a part of a large-scale ecological restoration program in Leivonmäki National Park, Finland (61ºN, 26ºE). The National Park was established in the year 2003, and it has a long history of intensive forest management. The amount of dead wood in natural forests in the geographic area is 50-80 m^3 ha^{-1} (Siitonen, 2001). At the beginning of the study, the study area retained about 10% of the natural amount of dead wood.

We selected 50 study plots, 0.25 ha (50×50 m) each, for the experiment from an area of 2×3 km. The plots were located in 80-120 year old Norway spruce (*Picea abies*) (23 plots) or Scots pine (*Pinus sylvestris*) (27 plots) stands with a few deciduous trees: birches (*Betula spp.*), grey alder (*Alnus incana*) and rowan (*Sorbus aucuparia*).

We established a two-factor experimental design supplemented with controls. We manipulated the amount of dead wood such that approximately 5 or 10 m^3 (corresponding to 20 and 40 m^3ha^{-1}) of the dominant tree species were felled with a chain saw. We also manipulated the spatial distribution of dead wood such that the added dead wood was either evenly distributed on the plot or aggregated at the center of the plot. There were ten replicates of each amount × distribution combination, and ten control plots with no manipulations. We randomized the treatments among the plots, and the fellings were conducted during winter 2003-2004. The realized amounts (± SD) of added dead wood were 5.00±0.56 m^3 (range 3.69-6.32 m^3) and 10.02±1.02 m^3 (range 8.12-11.57 m^3) in the low and high dead wood addition plots, respectively.

Natural dead wood data

We measured all natural dead wood with >5 cm diameter and >1.3 m length occurring on the plots in the year 2010. For each dead wood unit, we recorded the tree species and the decay stage according to a 5-stage classification (class one being recently died, hard wood, and class five being almost decomposed wood but still identifiable as a tree; Renvall, 1995). From whole dead trees, we measured the 1.3 m height diameter and length. From pieces of dead wood and whole trees that were partially outside the plot, we measured the diameters of the thicker and thinner end as well as the length of the piece. The volume of whole trees was calculated with the tree-specific equations of Laasasenaho (1982), and the volume of pieces with the formula of a truncated circular cone.

The volume of dead wood for the year 2003 was roughly estimated retrospectively from the year 2010 data by calculating the volume of late decay stages. To make the estimates more comparable the latest decay stage was excluded for the year 2010, since the latest decay stage for the year 2003 could not be estimated.

Polypore data

We collected polypore data before the treatments and yearly after the treatments until the year 2012. We systematically inventoried all added and natural dead wood units in October - early November each year. We defined the abundance of polypores as the number of occurrences, and all fruit bodies of a given species on one dead wood unit were regarded as one occurrence. Most of the polypore species were identifiable in the field, although in some cases we collected specimens for microscopic identification. The voucher specimens are deposited in the Natural History Museum of the University of Jyväskylä (JYV).

We used the Nordic concept of polypores, i.e. all poroid Aphyllophorales (Niemelä, 2005). As only coniferous dead wood was manipulated, we excluded species that grow exclusively on deciduous wood (Niemelä, 2005) and species that only occasionally utilize burned coniferous wood (Berglund, Jönsson, Penttilä, & Vanha-Majamaa, 2011).

Statistical analyses

First, we analyzed whether the dead wood addition had an effect on polypore abundance and species richness on all dead wood (not separating natural and added dead wood) or on natural dead wood. We used linear mixed models and entered year, treatment (five classes: control and each amount × distribution combination), tree species (spruce/pine) and their interactions as fixed factors. We added the study plot as a random factor and temporal correlation structure along years within the plot (an auto-regressive model of order 1, corAR1; Zuur, Ieno, Walker, Saveliev, & Smith, 2009, p. 149). If dead wood addition increases species richness *via* abundance, both abundance and species richness should be affected by dead wood addition, and species richness and abundance should also be positively correlated. Thus, we developed a complete set of models including all explanatory variable combinations for abundance and species richness, separately, and another model set for species richness with $\log_{10}$-transformed abundance as an additional explanatory variable. We used Akaike Information Criterion for small sample sizes (AICc) to compare the models within a set. The model with the smallest AICc is considered the best with respect to expected Kullback-Leibler information lost (Burnham & Anderson, 2002). In addition, we calculated R^2 values of occurrence-based species-accumulation curves (i.e. collector's curves) to study whether more occurrences resulted in more species within an individual plot using log-log, semi-log and ordinal relationships.

Second, we used linear mixed models to analyze the effects of the amount and distribution of the added dead wood on abundance and species richness (with and without abundance as an explanatory variable). In this next step, we analyzed the fungal communities on added dead wood and the natural dead wood separately. We entered year, amount (5/10 m^3), distribution (aggregated/even), tree species (spruce/pine) and their interactions as fixed factors, and study plot as a random factor. We added temporal correlation structure (corAR1) along years within the plot to the model. The best model in the set was not always apparent: the number of the reasonably good models ($d_i < 4$, where $d_i = \mathrm{AICc}_\mathrm{i} - \mathrm{AICc}_\mathrm{min}$) was 5 or more. Thus, we calculated the relative importance (I) of each variable for aiding the interpretation (Burnham & Anderson, 2002). We calculated I as a sum of Akaike weights over all of the models in which the variable appears (using the models for which $d_i < 4$). I ranges from zero (not important) to one (highly important).

Third, we analyzed whether adding dead wood affected the relationship between abundance and species richness by calculating rarefied species richness using individual-based rarefaction for each treatment × year combination. During the first years of the study, there were too few occurrences in some plots to allow calculation of the relationship for each plot × year combination separately. Therefore, we pooled all plots of a given treatment. We calculated rarefied species richness as the mean number of species accumulated in 20 randomly selected occurrences from 1,000 permutations of the data (Hurlbert, 1971).

Finally, we analyzed whether adding dead wood affected how fast species colonized the dead wood, i.e. the species-time relationship. Species-time relationship has been represented by a power function (Adler & Lauenroth, 2003)

$$S = cT^{w}$$

where S is the species richness, T is the temporal duration sampled, c is the intercept and w is the slope or the scaling exponent. We plotted the species richness of each plot against time, and compared log-log, semi-log and ordinal relationships across all curves using R^2 values. Since ordinal relationships generally gave the highest R^2 values (see Table S1 in Supporting Information), we used a simple linear model $S = c + wT$ to describe the relationship between time and species richness. The coefficient w describing the slope was used in general linear models as a response variable. First, we analyzed species-time relationships on i) all dead wood and ii) natural dead wood. We set treatment (five classes: control and each amount × distribution combination), tree species (spruce/pine) and their interactions as fixed factors. Second, we analyzed species-time relationships on i) added dead wood and ii) natural dead wood, excluded controls from the analysis, and set amount (5/10 m^3), distribution (aggregated/even), tree species (spruce/pine) and their interactions as fixed factors. As in other analyses, we used multimodel inference.

We conducted all analyses with R version 3.4.2 (R Development Core Team, 2017) and packages ‘MuMIn’ (Barton, 2015), ‘nlme’ (Pinheiro, Douglas, DebRoy, Sarkar, & the R Development Core Team, 2013) and ‘vegan’ (Oksanen et al., 2013).

RESULTS

Descriptive results

In total, we recorded 54 species during the study period. Forty-eight of the species occurred on natural dead wood and 38 species on added dead wood. Before the treatments in 2003, we recorded 245 occurrences and 20 species on natural dead wood. In the year 2012, we recorded a total of 2,593 occurrences and 45 species (Fig. 1). Of these 607 occurrences and 39 species were on natural dead wood whereas 1,986 occurrences but only 28 species were on added dead wood (Fig. 1).

The amount of natural dead wood (±SD) on the plots before the treatments was very low: 1.55 ± 0.83 m^3 (equaling 6.19 ± 3.32 $m^3 ha^{-1}$; Fig. S1), of which 88% consisted of coniferous trees. By the year 2010, the amount of natural dead wood had increased to 3.47 ± 2.14 m^3

(equaling 13.87±8.56 m^3ha^{-1}; Fig. S1) of which 90% consisted of coniferous trees. The amount of natural dead wood did not differ between the treatment classes before or after the dead wood addition (Table S2).

Changes attributed to added dead wood

First, we tested whether adding dead wood generally had an effect on species richness and abundance. For species richness on all dead wood, there was an interaction between year and treatment (Table 1). Together treatment, year and their interaction explained 71% of the variation in species richness (Table 1). When abundance was added to the modeling framework, the best model did not include treatment, and it was substantially better in terms of AICc values than the best model without abundance (1735.7 vs. 2008.0, respectively; Table 1). Moreover, 83% of the variation in abundance was explained by treatment, year, tree species and their interactions (Table 1). Hence, the effect of treatment on species richness was mediated largely by abundance. This was reflected also by the accumulation of species with increasing occurrences in individual plots: the R^2 values of these collector's curves were on average 0.93 and 0.89 at a log-log scale on natural and added dead wood, respectively (Table S3).

Second, we analyzed whether the amount or distribution of added dead wood affected species richness and abundance. The best models explaining species richness contained numerous interactions, and support for various variables. Together they explained 90% of the variation (Table 2). Model-averaged parameter estimates revealed that the effect of the amount and distribution of dead wood became visible towards the end of the study period (Table 3). During the years 2010-2012 sites with 10 m^3 dead wood had more species than sites with 5 m^3 dead wood (Fig. 2a). Moreover, in the years 2011 and 2012 evenly distributed dead wood had more species than aggregated dead wood (Fig. 2a). Although the amount remained in the model when abundance was included, the effect of distribution disappeared (Table 3).

Our third question was whether adding dead wood affected the relationship between abundance and species richness. We found that rarefied species richness on added dead wood was very low in comparison to that on natural dead wood at the beginning of the study. However, it increased steadily, nearly reaching the level of the rarefied species richness on natural dead wood by the end of the study period (Fig. 3, Fig. S2). By contrast, the relationships between abundance and species richness of the different amount × distribution treatments were virtually indistinguishable (Fig. 3a, Fig. S2a). This contradicts with the result that the amount of dead wood had an effect on species richness when abundance was included in the model. This is probably due to the large standard errors of the rarefaction.

Finally, when analyzing species-time relationships we noticed that almost all relationships were linear. Thus, species richness at a plot scale had not reached the asymptote, and we can expect to find more species in the future. Species-time relationships on all dead wood were affected by the treatment (Fig. 4). The best model included only treatment (df = 6, log-likelihood = -2.56, AICc = 19.1) which alone explained over 60% of the variation in the linear slopes between species richness and time. The second best model included also tree species (df = 7, loglikelihood = -2.09, AICc = 20.8, d = 1.8), and it was the only model with $d_i < 4$. All amount × distribution treatments had steeper relationships than controls (Fig. 4), and species-time relationships were also steeper with higher amount of added dead wood (Table 4).

Changes on natural dead wood

Treatment explained little variation in species richness on natural dead wood (Table 1). Moreover, the amount and distribution of added dead wood had no effect on species richness (Fig. 2b), and the relationships between abundance and species richness did not differ among control and treatments (Fig. 3, Fig. S2). Species-time relationship was best explained by the model containing only tree species: pine had a less steep species-time relationship than spruce (intercept: estimate = 0.41, SE = 0.05; pine: estimate = -0.19, SE = 0.07). Although this was clearly the best model (there was no model with $d_i < 4$), it explained only 10% of the variance in species richness. The amount or distribution of the added dead wood had no effect on species-time relationships on natural dead wood (Fig. 4) but again tree species had an effect (Table 4).

DISCUSSION

We showed that dead wood addition increased polypore species richness mainly through increasing abundances: a large amount of added dead wood resulted in higher abundances and a higher number of species than a small amount of added dead wood. This supports the view that the effect of energy on abundances is an important factor for species richness patterns (Storch et al., 2018), although in this study the reason was not decreased the extinction probabilities of populations (i.e. the more-individual hypothesis). Instead, colonization of the newly available resources resulted from random dispersal from the same regional species pool. Thus, our results are in accordance with the random sampling hypothesis.

However, a part of the effect of the amount of added dead wood on species richness was independent from the abundance. Indeed, heterogeneity of the resource plays a significant role in determining polypore species richness: For a given number of occurrences added dead wood contained *less* species than natural dead wood, especially during the first years of the study. This is most likely due to low diversity of the added dead wood, in terms of e.g. decay stages, which makes it a suitable resource for only a limited number of species (Komonen et al., 2014; Pasanen, Junninen, & Kouki, 2014). Thus, our results are in concert with previous work showing that in addition to abundance, habitat heterogeneity is an important factor behind species-energy relationship (Hurlbert, 2004).

The distribution of the added dead wood was hypothesized to affect species richness by changes in numbers of resource type. For the case when dead wood was evenly distributed, all or most of the logs touched the ground. When dead wood was spatially aggregated, the logs formed a stack where only a few logs touched the ground. Therefore, we expected more variation in the physical conditions of logs within the aggregated treatment, and consequently more resource types for more species. However, species richness was higher when dead wood was evenly distributed. It may be that the aggregated dead wood was partially unsuitable for polypores (i.e. too dry on the top of the stack or too cold, shaded and wet in the bottom and inside the stack). This is supported by the fact that the effect of spatial distribution was mediated solely by increased abundance on evenly distributed dead wood compared with aggregated dead wood.

Species richness on natural or added dead wood had not reached the asymptote during the study period, meaning that species richness is likely to increase in the future. Although polypores in general are good dispersers (Komonen & Müller, 2018) certain species may have limited dispersal capacity (Edman, Gustafsson, Stenlid, Jonsson, & Ericson, 2004). At a plot scale, the increase in species richness is likely a result from the changes of the chemical and physical quality of the dead wood. While many species colonize recently created dead wood (Niemelä, Renvall, & Penttilä, 1995), or are present already in the living trees and start to grow aggressively after tree death (Parfitt, Hunt, Dockrell, Rogers, & Boddy, 2010), other species rely on the work of these primary decayers (Heilmann-Clausen, 2001). In our study, the first such species, red-listed *Antrodiella parasitica* (VU; Kotiranta, Junninen, Saarenoksa, Kinnunen, & Kytövuori, 2010), an obligatory successor species of common *Trichaptum abietinum*, did not occur until eight years after the treatments. Indeed, the species richness of wood-decaying fungi tends to be maximized during the middle decay stages (Junninen & Komonen, 2011), and our analysis showed that the differences between the different dead wood additions (small vs. large amount, aggregated vs. even distribution) became visible only towards the end of the study. This emphasizes that long-term monitoring schemes are necessary to detect the true effect of resource addition on polypore species richness.

During the study, the amount of natural dead wood increased substantially. Because the tree felling may lead to an increase of pathogens, bark beetles and other tree-killing agents (Komonen & Kouki, 2008), we expected treatments to cause an increase of natural dead wood. Although we observed this in some plots, statistical tests did not show a difference in the amount of natural dead wood or in the species richness on natural dead wood between the treatments. Thus, the increase in the amount of natural dead wood and associated species richness was primarily due to natural succession. Without natural dead wood formation, the positive effects of resource addition would not be long-lasting: only continuous supply of new resources enables wood-decaying fungi to persist in the landscape.

The dead wood addition benefited mainly the species still persisting in the resource depleted landscape. Nevertheless, the importance of such species should not be undervalued. They are often important ecosystem engineers, these species play a major role in e.g. nutrient cycling, and act as pioneering decayers for rarer species. Species richness increased irrespective of the magnitude of the pulse, but more was clearly more: if we want to benefit a larger number of polypore species, a larger resource pulse does this a somewhat better than a small one.

SUPPORTING INFORMATION

Table S1 R^2 values for the different relationships between species richness and time at plot scale

Table S2 Parameter estimates from the linear mixed models explaining the amount of natural dead wood

Table S3 R^2 values of the collector's curves

Fig. S1 The amount of natural dead wood before and after the treatments

Fig. S2 Rarefied species richness (with standard errors) on added and natural dead wood

AUTHORS' CONTRIBUTIONS

JK and TT designed the experiment; PH and TT were responsible for the data collection; ME and TT analyzed the data and led the writing of the manuscript; PH and JK contributed substantially to the writing process and all authors gave final approval for publication.

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Data accessibility Data available via the University of Jyväslylä JYX Digital Repository https://doi.org/10.17011/jyx/dataset/62666 (Elo, Halme, Toivanen, & Kotiaho, 2019).

REFERENCES

Abrams, P. A. (1995). Monotonic or unimodal diversity productivity gradients: what does competition theory predict? *Ecology*, *76*(7), 2019–2027.

Adler, P. B., & Lauenroth, W. K. (2003). The power of time: Spatiotemporal scaling of species diversity. *Ecology Letters*, *6*(8), 749–756. doi:10.1046/j.1461-0248.2003.00497.x

Barton, K. (2015). MuMIn: Multi-Model Inference. Retrieved from http://cran.r-project.org/package=MuMIn

Berglund, H., Jönsson, M. T., Penttilä, R., & Vanha-Majamaa, I. (2011). The effects of burning and dead wood creation on the diversity of pioneer wood-inhabiting fungi in managed boreal spruce forests. *Forest Ecology and Management*, *261*, 1293–1305.

Boddy, L., Frankland, J. C., & van West, P. V. (2008). *Ecology of saprotrophic basidiomycetes*. Amsterdam, Netherlands: Elsevier.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference. A practical information-theoretic approach.* (Vol. 2). USA: Springer Science + Business Media, LLC.

Drever, M. C., Goheen, J. R., & Martin, K. (2009). Species-energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. *Ecology*, *90*, 1095–1105.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B. G., & Ericson, L. (2004). Spore deposition of wood-decaying fungi: Importance of landscape composition. *Ecography*, *27*(1), 103–111. doi:10.1111/j.0906-7590.2004.03671.x

Elo, M., Halme, P., Toivanen, T., & Kotiaho, J. S. (2019). *Research data of the article: Elo et al. 2019 Species richness of polypores can be increased by supplementing dead wood resource into a boreal forest ecosystem. JYX Digital Repository*.

Evans, K. L., Jackson, S. F., Greenwood, J. J. D., & Gaston, K. J. (2006). Species traits and the form of individual species-energy relationships. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *273*(1595), 1779–1787. doi:10.1098/rspb.2006.3487

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *80*(1), 1–25. doi:10.1017/S1464793104006517

Field, R., Hawkins, B. A., Cornell, H. V, Currie, D. J., Diniz-Filho, J. A. F., Guégan, J.-F., … Turner, J. R. G. (2009). Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, *36*(1), 132–147. Retrieved from http://dx.doi.org/10.1111/j.1365-2699.2008.01963.x

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics*, *33*, 1–23.

Halme, P., Allen, K. A., Auniņš, A., Bradshaw, R. H. W., Brumelis, G., Čada, V., … Zin, E. (2013). Challenges of ecological restoration: Lessons from forests in northern Europe. *Biological Conservation*, *167*, 248–256. doi:10.1016/j.biocon.2013.08.029

Heilmann-Clausen, J. (2001). A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. *Mycological Research*, *105*(5), 575–596. doi:10.1017/S0953756201003665

Heilmann-Clausen, J., Aude, E., & Christensen, M. (2005). Cryptogam communities on decaying deciduous wood – does tree species diversity matter? *Biodiversity and Conservation*, *14*, 2061–2078.

Honkanen, M., Roberge, J.-M., Rajasärkkä, A., & Mönkkönen, M. (2010). Disentangling the effects of area, energy and habitat heterogeneity on boreal forest bird species richness in protected areas. *Global Ecology and Biogeography*, *19*, 61–71. doi:10.1111/j.1466-8238.2009.00491.x

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton, New Jersey: Princeton Monographs in Population Biology, Princeton University Press.

Hurlbert, A. H. (2004). Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, *7*(8), 714–720. doi:10.1111/j.1461-0248.2004.00630.x

Hurlbert, S. H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, *52*, 577–586.

Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds of Animals? *The American Naturalist*, *93*(870), 145–149.

Junninen, K., & Komonen, A. (2011). Conservation ecology of boreal polypores: A review. *Biological Conservation*, *144*(1), 11–20. doi:10.1016/j.biocon.2010.07.010

Komonen, A., Halme, P., Jäntti, M., Koskela, T., Kotiaho, J. S., & Toivanen, T. (2014). Created substrates do not fully mimic natural substrates in restoration: The occurrence of polypores on spruce logs. *Silva Fennica*, *48*(1). doi:10.14214/sf.980

Komonen, A., & Kouki, J. (2008). Do restoration fellings in protected forests increase the risk of bark beetle damages in adjacent forests? A case study from Fennoscandian boreal forest. *Forest Ecology and Management*, *255*(11), 3736–3743. doi:10.1016/j.foreco.2008.03.029

Komonen, A., & Müller, J. (2018). Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, *32*(3), 535–545. doi:10.1111/cobi.13087

Kotiranta, H., Junninen, K., Saarenoksa, R., Kinnunen, J., & Kytövuori, I. (2010). Aphyllophorales & Heterobasidiomycetes. In P. Rassi, E. Hyvärinen, A. Juslén, & I. Mannerkoski (Eds.), *The 2010 Red List of Finnish Species* (pp. 249–263). Helsinki, Finland: Ympäristöministeriö & Suomen Ympäristökeskus.

Laasasenaho, J. (1982). Taper curve and volume functions for pine, spruce and birch. *Communicationes Instituti Forestalis Fenniae*, *108*, 1–74.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., … Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, *82*(9), 2381–2396.

Niemelä, P. (2005). Polypores - lignicolous fungi. *Norrlinia*, *13*, 1–320.

Niemelä, T., Renvall, P., & Penttilä, R. (1995). Interactions of fungi at late stages of wood decomposition. *Annales Botanici Fennici*, *32*(3), 141–152.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2013). vegan: Community Ecology Package. Retrieved from http://cran.r-project.org/package=vegan

Parfitt, D., Hunt, J., Dockrell, D., Rogers, H. J., & Boddy, L. (2010). Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecology*, *3*(4), 338–346. doi:10.1016/j.funeco.2010.02.001

Pasanen, H., Junninen, K., & Kouki, J. (2014). Restoring dead wood in forests diversifies wood-decaying fungal assemblages but does not quickly benefit red-listed species. *Forest Ecology and Management*, *312*, 92–100. doi:10.1016/j.foreco.2013.10.018

Pinheiro, J., Douglas, B., DebRoy, S., Sarkar, D., & the R Development Core Team. (2013). nlme: Linear and Nonlinear Mixed Effects Models.

R Development Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Rassi, P., Hyvärinen, E., Juslén, A., & Mannerkoski, I. (2010). *The 2010 Red List of Finnish Species*. Helsinki: Ympäristöministeriö & Suomen Ympäristökeskus.

Renvall, P. (1995). Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. *Karstenia*, *35*, 1–51.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as a example. *Ecological Bulletins*, *49*, 11–41.

Spribille, T., Thor, G., Bunnell, F. L., Goward, T., & Björk, C. R. (2008). Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific

Northwest and Fennoscandia. *Ecography*, *31*, 741–750.

Srivastava, D. S., & Lawton, J. H. (1998). Why More Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities. *American Naturalist*, *152*(4), 510–529.

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity-diversity relationship. *Ecology Letters*. doi:10.1111/ele.12941

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., … Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, Vol. 30, p. doi:10.1146/annurev.ecolsys.30.1.257

Wright, D. H. (1983). Species-energy theory : an extension of species-area theory. *Oikos*, *41*, 496–506.

Yang, L. H., Bastow, J. L., Spence, K. O., & Wright, A. N. (2008). What Can We Learn from Resource Pulses? *Ecology*, *89*(3), 621–634.

Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N., & Spence, K. O. (2010). A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs*, *80*(1), 125–151. doi:10.1890/08-1996.1

Yee, D. A., & Juliano, S. A. (2007). Abundance matters: a field experiment testing the more individuals hypothesis for richness-productivity relationships. *Oecologia*, *153*(1), 153–162.

Zuur, A. F., Ieno, E. N., Walker, N. j, Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, N.Y.: Springer Science + Business Media, LLC.

Table 1 Linear mixed models with species richness (with and without abundance as an explanatory variable) and abundance on all and natural dead wood as response variables. Treatment (five classes: control and each amount × distribution combination), tree (two classes: spruce/pine), year (ten classes: 2003-2012) and their interactions were set as explanatory variables. R^2 values (representing the variation explained by the fixed factors), degrees of freedom (df), log-likelihood, and second-order Akaike Information Criteria (AICc) are shown for the best ($d < 4$) models

Dead wood	Response variable	R^2	df	logLik	AICc	*d*	(Int)	Treatment	Tree	Year	Abundance	Treatment × Year	Tree × Year	Treatment × Tree
All	Species richness w/o abundance	0.71	53	-944.6	2008.0	0.0	2.8	+		+	*NA*	+		
		0.71	54	-943.8	2009.0	1.0	3.0	+	+	+	*NA*	+		
	Species richness w/ abundance	0.85	24	-842.6	1735.7	0.0	-1.2		+	+	2.6		+	
	Abundance	0.83	67	-257.1	669.4	0.0	1.6	+	+	+	*NA*	+	+	+
		0.81	63	-262.5	669.5	0.1	1.5	+	+	+	*NA*	+	+	
Natural	Species richness w/o abundance	0.18	14	-974.8	1978.4	0.0	3.7		+	+	*NA*			
		0.16	13	-976.4	1979.5	1.1	3.2			+	*NA*			
	Species richness w/ abundance	0.79	15	-715.9	1462.7	0.0	-1.4		+	+	2.8			
		0.78	14	-718.3	1465.5	2.8	-1.1			+	2.7			
	Abundance	0.25	23	-344.4	737.2	0.0	1.6		+	+	*NA*		+	

Table 2 The importance (*I*) of the amount of added dead wood, the distribution of added dead wood, tree species, year and their interactions on species richness (with and without abundance as an explanatory variable) and abundance on added and natural dead wood. Values towards one indicate high importance and values towards zero indicate non-importance. The number in the brackets shows the number of linear mixed models used in calculating *I* (see Statistical analyses for further information). R^2 values are presented for the best model judged by AICc for each response variable, and the variables included in these best models are highlighted in bold

Dead wood	Response variable	R^2	Amount	Dis	Tree	Year	Abundance	Amount × Year	Dis × Year	Tree × Year	Amount × Tree	Dis × Tree	Amount × Dis
Added	Species richness w/o abundance (10)	0.92	**1**	**0.8**	**1**	**1**	*NA*	**1**	0.36	**1**	0.17	0.13	0.12
	Species richness w/ abundance (10)	0.93	**0.96**	0.32	**1**	**1**	**1**	0.37	0.13	**1**	0.18	0.04	
	Abundance (8)	0.95	**1**	**1**	**1**	**1**	*NA*	**0.91**		**1**	0.2	**0.52**	0.17
Natural	Species richness w/o abundance (11)	0.22	0.33	0.44	**0.67**	**1**	*NA*				0.03	0.1	
	Species richness w/ abundance(12)	0.79	0.43	0.37	**0.57**	**1**	**1**	0.03			0.04	0.13	
	Abundance (6)	0.27	0.26	0.53	**1**	**1**	*NA*			**1**		0.28	

Table 3 Model-averaged parameter estimates and their 97% confidence intervals (CIs) from the linear mixed models explaining species richness (with and without abundance as an explanatory variable) and abundance of polypores on added dead wood. The amount of added dead wood (5/10 m^3), the distribution of added dead wood (aggregated/even), tree species (spruce/pine), year (2003-2012) and their interactions were used as fixed factors and the plot as a random factor. The parameter estimates are shown in bold if the 97% CIs do not include zero. Amount of 5 m^3, aggregated distribution, spruce and the year 2003 were used as baselines. Some of the variables do not have parameter estimates since only the models with d_i < 4 were used in model averaging

	Species richness w/o abundance			Species richness w/ abundance			Abundance		
	Estimate	97% Cis		Estimate	97% Cis		Estimate	97% Cis	
(Intercept)	-0.06	-0.70	0.58	-0.08	-0.62	0.45	-0.15	-0.42	0.11
Am10	0.00	-0.71	0.71	0.20	-0.37	0.77	0.01	-0.32	0.35
Even	0.14	-0.47	0.75	-0.02	-0.49	0.45	**0.29**	**0.02**	**0.56**
Pine	0.01	-0.70	0.72	-0.01	-0.66	0.64	0.05	-0.27	0.37
Year2004	0.00	-0.70	0.70	0.00	-0.60	0.60	0.00	-0.19	0.19
Year2005	**0.92**	**0.12**	**1.71**	-1.11	-1.99	-0.22	**1.84**	**1.61**	**2.07**
Year2006	**1.98**	**1.14**	**2.83**	-0.77	-1.83	0.29	**2.57**	**2.31**	**2.82**
Year2007	**4.16**	**3.33**	**4.99**	0.83	-0.37	2.03	**3.13**	**2.86**	**3.40**
Year2008	**5.11**	**4.28**	**5.95**	1.30	-0.02	2.61	**3.39**	**3.11**	**3.66**
Year2009	**5.97**	**5.12**	**6.82**	**2.02**	**0.66**	**3.37**	**3.53**	**3.26**	**3.81**
Year2010	**5.80**	**4.97**	**6.63**	**2.08**	**0.77**	**3.39**	**3.54**	**3.27**	**3.82**
Year2011	**6.43**	**5.45**	**7.41**	**2.71**	**1.33**	**4.09**	**3.70**	**3.43**	**3.97**
Year2012	**7.38**	**6.38**	**8.37**	**3.69**	**2.28**	**5.10**	**3.73**	**3.45**	**4.00**
Am10 × Year2004	0.00	-0.77	0.77	0.00	-0.73	0.73	0.00	-0.22	0.22
Am10 × Year2005	0.20	-0.67	1.07	0.07	-0.75	0.89	0.12	-0.14	0.38
Am10 × Year2006	0.50	-0.40	1.40	0.11	-0.74	0.96	**0.37**	**0.09**	**0.64**
Am10 × Year2007	0.81	-0.10	1.72	0.37	-0.49	1.22	**0.41**	**0.13**	**0.69**
Am10 × Year2008	0.31	-0.60	1.22	-0.20	-1.06	0.66	**0.47**	**0.19**	**0.75**
Am10 × Year2009	0.46	-0.45	1.37	-0.04	-0.90	0.82	**0.46**	**0.18**	**0.75**
Am10 × Year2010	**1.16**	**0.25**	**2.07**	0.67	-0.20	1.53	**0.46**	**0.18**	**0.74**
Am10 × Year2011	**1.37**	**0.46**	**2.28**	**0.91**	**0.05**	**1.77**	**0.43**	**0.14**	**0.71**
Am10 × Year2012	**1.61**	**0.70**	**2.52**	**1.13**	**0.26**	**1.99**	**0.45**	**0.17**	**0.73**
Pine × Year2004	0.00	-0.77	0.77	0.00	-0.74	0.74	0.00	-0.22	0.22
Pine × Year2005	-0.52	-1.40	0.35	**1.18**	**0.22**	**2.13**	-1.52	-1.78	-1.25
Pine × Year2006	-0.01	-0.91	0.89	0.71	-0.17	1.59	-0.63	-0.91	-0.35
Pine × Year2007	-0.09	-1.00	0.82	-0.06	-0.93	0.81	-0.01	-0.29	0.28
Pine × Year2008	-0.57	-1.49	0.34	-0.35	-1.22	0.52	-0.21	-0.50	0.08
Pine × Year2009	-0.11	-1.03	0.80	0.06	-0.81	0.93	-0.15	-0.44	0.14

Pine × Year2010	-0.63	-1.55	0.28	-0.31	-1.18	0.57	-0.25	-0.54	0.04
Pine × Year2011	**1.28**	**0.36**	**2.19**	**1.54**	**0.66**	**2.41**	-0.18	-0.47	0.11
Pine × Year2012	0.38	-0.54	1.29	0.65	-0.23	1.53	-0.18	-0.47	0.11
Even × Year2004	0.00	-0.76	0.76	0.00	-0.73	0.73			
Even × Year2005	-0.05	-0.90	0.80	-0.16	-0.98	0.65			
Even × Year2006	0.40	-0.48	1.28	0.12	-0.72	0.95			
Even × Year2007	0.20	-0.69	1.09	-0.19	-1.03	0.66			
Even × Year2008	-0.15	-1.04	0.74	-0.47	-1.32	0.37			
Even × Year2009	-0.35	-1.24	0.54	-0.72	-1.57	0.12			
Even × Year2010	0.10	-0.79	0.99	-0.26	-1.11	0.58			
Even × Year2011	**1.00**	**0.11**	**1.89**	0.62	-0.23	1.47			
Even × Year2012	**1.05**	**0.16**	**1.94**	0.71	-0.14	1.55			
Even × Pine	-0.09	-0.73	0.55	0.19	-0.35	0.72	-0.24	-0.58	0.10
Am10 × Even	0.05	-0.58	0.69				0.05	-0.30	0.39
Am10 × Pine	-0.04	-0.69	0.61	-0.14	-0.67	0.39	0.09	-0.26	0.44
Abundance				**1.12**	**0.81**	**1.42**			

Table 4 Model-averaged parameter estimates, their 97% Confidence Intervals (CIs) and the importance (*I*) from the linear mixed models describing the effect of the amount and distribution of added dead wood, tree species and their interactions on *w*-values (the slope of the species-time relationship) on added and natural dead wood. Parameter estimates are shown in bold if their 97% CIs do not encompass zero. *I*-values towards one indicate high importance and values towards zero indicate non-importance. The number in the brackets shows the number of linear mixed models used in calculating model-averaged parameter estimates and Importance (see Statistical analyses for further information). *I* is not meaningful to the intercept.

	Added dead wood (9)				Natural dead wood (5)			
Variable	Estimate	97% CIs		*I*	Estimate	97% CIs		*I*
(Intercept)	**0.92**	**0.79**	**1.06**	**-**	**0.40**	**0.26**	**0.54**	**-**
Am10	**0.20**	**0.06**	**0.34**	1.00	0.07	-0.11	0.25	0.61
Even	0.06	-0.08	0.20	0.65	0.00	-0.07	0.07	0.20
Pine	0.06	-0.09	0.21	0.61	**-0.19**	**-0.35**	**-0.03**	1.00
Am10 × Even	0.00	-0.08	0.08	0.14				
Even × Pine	0.00	-0.05	0.06	0.11				
Am10 × Pine	-0.01	-0.13	0.10	0.05	0.00	-0.10	0.11	0.11

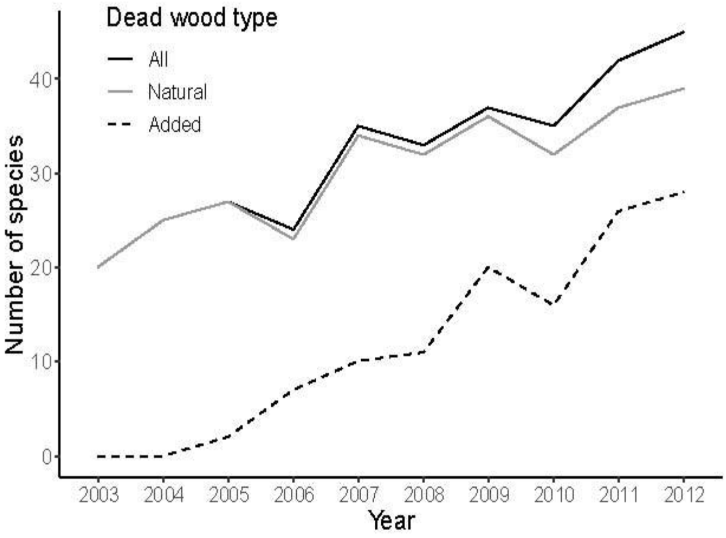
FIGURE LEGENDS

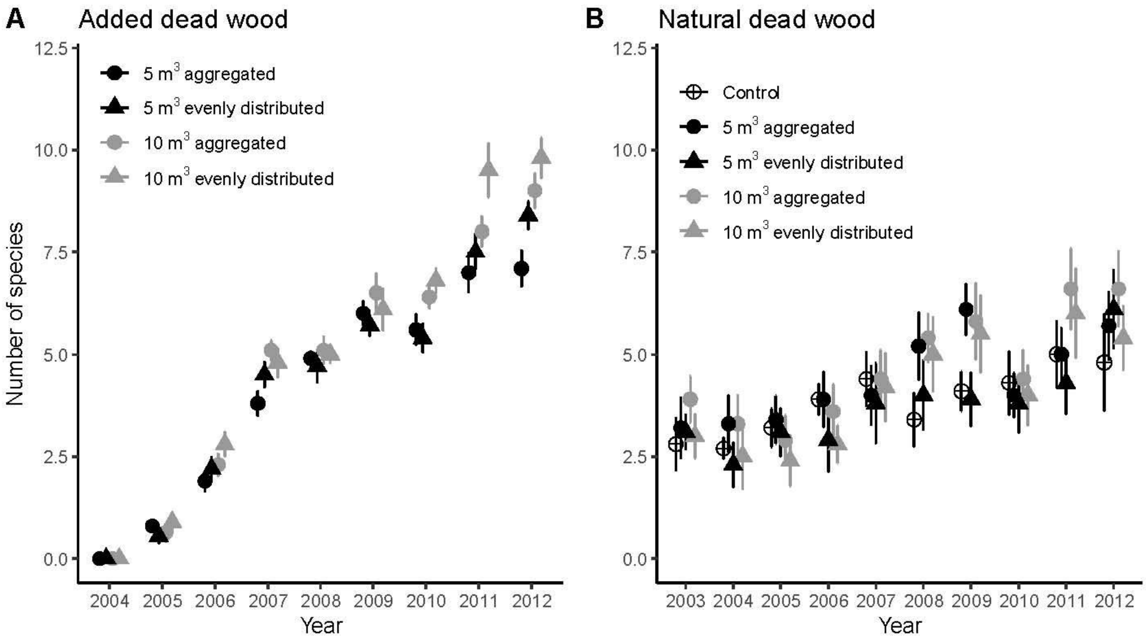
Fig. 1 Yearly total polypore species richness on all dead wood, natural dead wood and added dead wood during the study period at the landscape scale

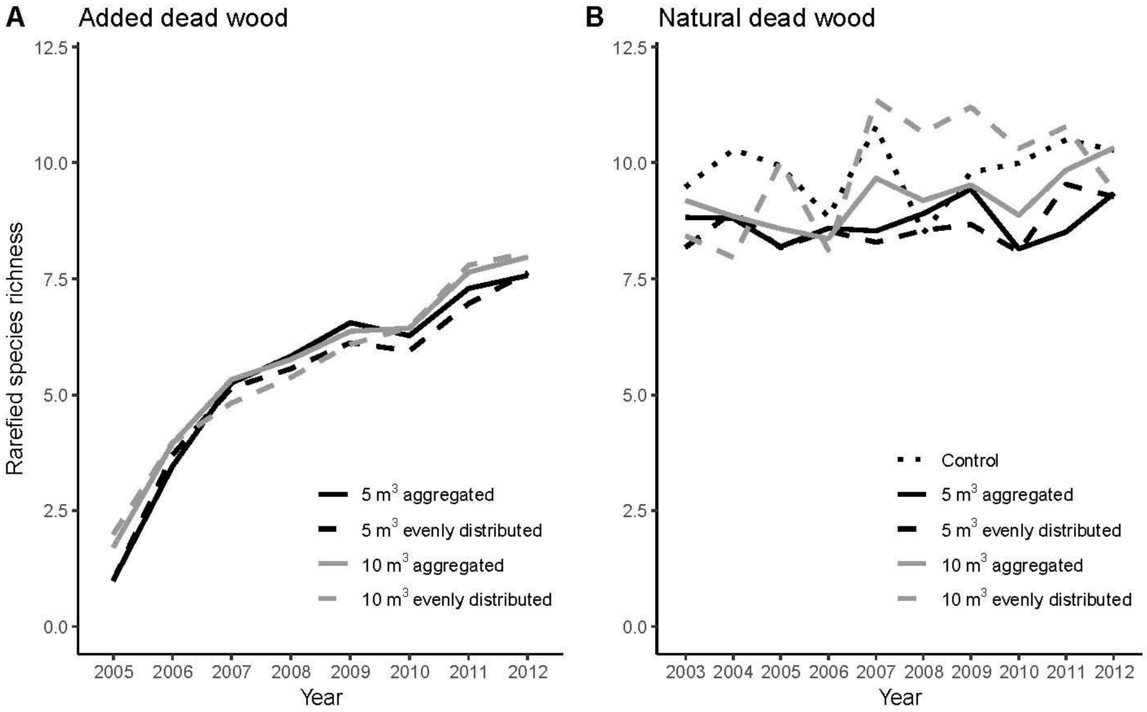
Fig. 2 The effect of the year and treatment on the species richness of polypores on added (A) and natural (B) dead wood. The symbols describe the mean (±SE) species richness in 10 replicate plots for control (natural dead wood only) and each of the four treatments

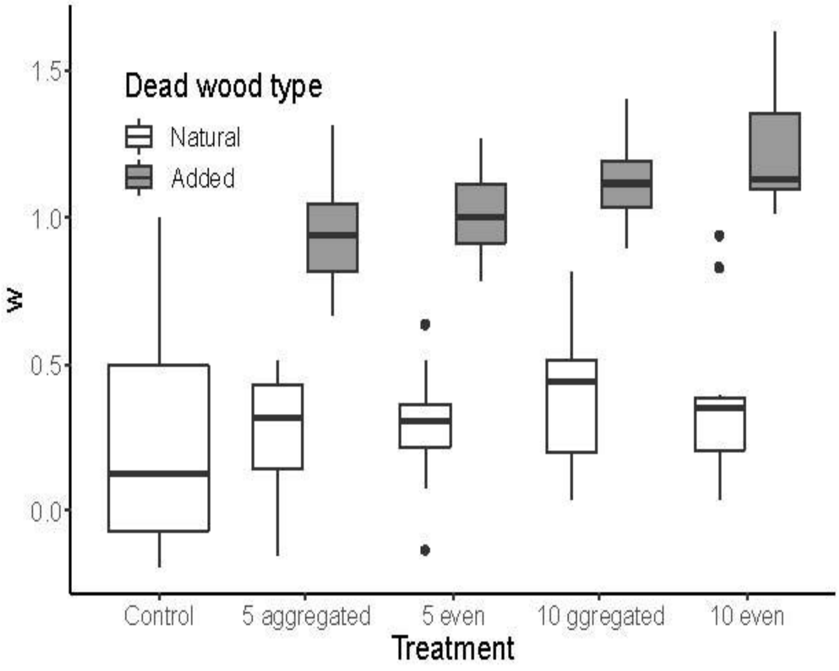
Fig. 3 Relationship between the number of species and abundance on added (A) and natural (B) dead wood. Rarefied species richness is the mean number of species accumulated in 20 randomly selected occurrences from the pooled data containing all ten sites of the control (only natural dead wood) and the four treatments. See Fig. S2 for standard errors

Fig. 4 Species-time relationship on natural and added dead wood during the study period on individual study plots within each treatment. The y-axis (w) is the slope in the equation describing the linear relationship between time and species richness calculated for each individual plot ($S = c + wT$, where S = species richness, c = constant, T = time). The boxplot represents 25%, 50% and 75% quantiles


Dead wood type
All
Natural
Added
Number of species
0
10
20
30
40
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
Year


A
Added dead wood
5 m^3 aggregated
5 m^3 evenly distributed
10 m^3 aggregated
10 m^3 evenly distributed
Number of species
0.0
2.5
5.0
7.5
10.0
12.5
2004
2005
2006
2007
2008
2009
2010
2011
2012
Year
B
Natural dead wood
Control
5 m^3 aggregated
5 m^3 evenly distributed
10 m^3 aggregated
10 m^3 evenly distributed
0.0
2.5
5.0
7.5
10.0
12.5
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
Year


A
Added dead wood
B
Natural dead wood
Rarefied species richness
12.5
10.0
7.5
5.0
2.5
0.0
2005 2006 2007 2008 2009 2010 2011 2012
2003 2004 2005 2006 2007 2008 2009 2010 2011 2012
Year
Control
5 m^3 aggregated
5 m^3 evenly distributed
10 m^3 aggregated
10 m^3 evenly distributed


Dead wood type
Natural
Added
w
1.5
1.0
0.5
0.0
Control
5 aggregated
5 even
10 ggregated
10 even
Treatment