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Rat invasion of islands alters fungal community structure, but not wood decomposition rates

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Introduced animals can indirectly affect decomposers through trophic cascades and habitat modifications, but whether their effects are strong enough to influence both the structure and function of decomposer communities remains unclear. We conducted an experiment on rat-invaded and rat-free islands off the coast of New Zealand to determine whether introduced rats affected the structure and function of wood-decomposing fungi. Gamma-irradiated branch segments from a single tree were placed on the forest floor on nine rat-invaded and nine rat-free islands, and fungal community structure and wood decomposition rates measured after two years of in situ decomposition. We found significant differences in fungal community structure in the wood between rat-invaded and rat-free islands. Furthermore, there was a significant correlation between fungal community structure and wood decomposition rate on rat-free islands but not on rat-invaded islands, because of decreased variability in decomposition rates on invaded islands. Despite these differences between rat-free and rat-invaded islands, mean decomposition rates were indistinguishable between the two sets of islands. These results suggest that there may be a great deal of functional redundancy in fungal communities and that removing rats from islands could reverse the rat-induced changes that we observed in the relationship between the structure and function of decomposer communities.

Introduced species can profoundly affect terrestrial ecosystems (Elton 1958, Vitousek et al. 1997). Many studies have focused on introduced plants because plants can directly interact with other functionally important organisms such as fungi and bacteria (Kourtev et al. 2002, Wolfe and Klironomos 2005, van der Putten et al. 2007). However, it is increasingly recognized that introduced animals can exert indirect effects through trophic cascades and habitat modifications (O'Dowd et al. 2003, Sanders et al. 2003, Croll et al. 2005, Green et al. 2011), including effects on the fungi and bacteria that drive decomposition (Fukami et al. 2006, Eisenhauer et al. 2011). What remains unclear is whether introduced animals primarily affect the structure of fungal and bacterial communities or if they also alter the functional role of these communities. The answer is likely to depend on the extent of functional redundancy in the invaded communities. If fungal and bacterial species are functionally unique, changes in species composition caused by introduced animals should lead to alteration in the function of the affected community. On the other hand, if many species are functionally redundant, changes in species composition may not affect the function of the community as a whole. The possibility that introduced animals indirectly affect both the structure and function of decomposers has rarely been tested.

In this study, we investigated the response of wood-decomposing fungi to rat invasion (*Rattus rattus* and *R. norvegicus*), using the same system of New Zealand islands as that used by Fukami et al. (2006). Previously, we showed that predation of seabirds by rats caused changes in soil fauna, leaf litter decomposition, and plant nutrient concentrations due to reduced input of seabird-transferred marine nutrients (Fukami et al. 2006, Wardle et al. 2007, 2009, Mulder et al. 2009, Towns et al. 2009). Here, we use the results of a two-year manipulative experiment to compare the structure (richness and composition) and function (decomposition rates) of wood-decomposing fungi between rat-invaded and rat-free islands. Fungal decomposition of wood can be affected by the physical and chemical properties of soil as well as by the local soil biota (Cooke and Rayner 1984). Because rats extirpate seabird populations and therefore reduce marine-derived nutrient inputs and change the soil physical environment (Fukami et al. 2006), we hypothesized that rats would affect fungal community structure and reduce rates of decomposition indirectly via their effects on seabirds. In addition, because priority effects can be strong in fungal communities (Kennedy and Bruns 2005, Dickie et al. 2012, Peay et al. 2012), we examined the effect of initial fungal composition

on community structure and decomposition, which we expected to have the potential to obscure effects of rat invasion by increasing variability in the community assembly process.

Methods

Study system

The study was carried out on a set of warm temperate islands located in northern New Zealand. We used nine islands invaded by rats and nine islands that had never been invaded by rats (Fukami et al. 2006, Wardle et al. 2007, 2009, Towns et al. 2009). The islands were comparable in size, isolation, climate and geology, but differed in the history of rat invasion. For details on island characteristics, see Fukami et al. (2006) and Supplementary material Appendix A1.

Experimental design

Previous work has shown that rat invasion alters litter decomposition rates through changes in plant nutrient quality (Fukami et al. 2006, Wardle et al. 2009). Thus, to isolate the effects of fungal community structure per se on decomposition from potential plant quality effects, we used wood from a single tree of *Melicytus ramiflorus* (Violaceae), the most widespread tree species across the islands in our study. A *M. ramiflorus* tree grown on the campus of Landcare Research at Lincoln, New Zealand (172°48′E, 43°64′S), was felled to provide the substrate for the experiment on the islands. Branches from this tree were cut to 15 cm length, with diameters ranging in size between approx. 2 and 10 cm, and gamma-irradiated to sterilize. Branches of this size were amenable to experimental manipulation, but would still persist for the two-year duration of the experiment.

Initial fungal composition for each branch was manipulated by using downed woody debris of *M. ramiflorus* collected on site on each island as fungal inocula. Inocula were collected locally on each island rather than using a single inoculum source for the study in order to avoid introducing foreign organisms to these islands. *Melicytus ramiflorus* woody debris was ground into sawdust using a Waring blender and then inserted into holes (approx. 1 cm diameter and 0.5 cm depth) drilled onto each 15 cm branch segment. To create variation in initial fungal community structure, the inoculum was sourced from either 10 separate wood pieces pooled together (hereafter called 'pooled'), a single piece of wood ('single'), or no inoculation ('control'). Each treatment was replicated five times for a total of 15 branches per island. Branches were randomly assigned to islands and the inoculation treatments. Each branch was sealed in coarse mesh (mesh size: 4 mm), tagged and staked to the forest floor for relocation. All branches were placed on the forest floor, within the vegetation plots used by Fukami et al. (2006), between April and May of 2004 and collected for analysis between April and May of 2006.

As a measure of ecosystem function we recorded initial and final wet and dry weights for each wood piece and calculated the proportion of mass lost by decomposition as 1 – (final dry weight/initial dry weight). Additional functional measures, such as extracellular enzymes or gene expression, may provide some mechanistic insight into the decomposition process, but are often highly variable in space and time (Šnajdr et al. 2008, Kellner et al. 2009) and also have additional cell regulatory function not directly related to ecosystem function (Nagai et al. 2003, Adams 2004). Thus, single time point measures of enzymes or genes may not be reflective of the overall decay process on long-lasting woody substrates. For this reason we chose to measure total wood decomposition as a time-integrated measure of the total effect of fungal community activity on a key ecosystem process.

Molecular identification

The fungal community from each inoculum and each experimental unit was characterized using terminal restriction fragment length polymorphism (T-RFLP) based on peak profiles, without attempting to identify species (Dickie and FitzJohn 2007). In brief, the surface bark of each experimental unit was removed by an ethanol flamed blade, and on the exposed inner surface of wood, ethanol flamed 1.5-mm drill bits were used to obtain sawdust from each experimental replicate. Approximately 5.5 mg of sawdust from logs and the initial inoculum was used to extract DNA. Polymerase chain reaction was carried out using standard methods (Dickie et al. 2012) with the labeled primers ITS1F-FAM (Gardes and Bruns 1993) and ITS4-VIC (White et al. 1990). PCR products were cleaned using a PCR purification kit and then digested with the restriction enzymes HpyCH4IV and HaeIII at 37°C for 4 h. Restriction digests were then denatured with highly de-ionized formamide, and $0.1\times$ diluted samples run through capillary electrophoresis on a genetic analyzer with MapMaker 1000 standard. For each primer-enzyme combination, raw T-RFLP peaks were binned into operational taxonomic units (OTUs) using complete linkage hierarchical clustering with a bin size of 2.5 base pairs. Pairwise sample similarities were calculated separately for each of the four primer-enzyme combinations based on the shared and not-shared peaks using β_{sim} distances (Koleff et al. 2003), with sample similarities averaged across the four primer–enzyme combinations. Similarly, OTU richness was estimated as the number of clustered peaks, averaged across all four primer-enzyme combinations.

Data analysis

Because of the hierarchical nature of the experiment, we adopted a linear mixed-effects modeling approach using the top–down method suggested by Zuur et al. (2009). Starting with the full model, likelihood ratio tests were used first to determine the most appropriate error structure (e.g. what types of random effects to include). After determining the best error structure, likelihood ratio tests were further used to select the best combination of predictor variables. This was done in a sequential process, starting with the highest order terms, and comparing 'likelihood scores' between a full model and all reduced models where a single

term of a given order had been eliminated. The term with the least contribution to model fit was eliminated to generate a new full model which was then compared with all the remaining reduced models. This process was iterated until the most parsimonious model was achieved. Parameters for the final model were then estimated using restricted maximum likelihood (REML). Rat invasion status was treated as a nested variable throughout our analyses, with the islands considered the unit of replication, to avoid pseudoreplication. Because the inoculation treatments were collected separately at each island we were able to test whether species richness varied between starting inoculum used for single- and pooled-inocula treatments and sourced from rat invaded and uninvaded islands. In addition we tested whether inoculation treatment, rat invasion status, and initial wood weight affected fungal species richness in wood branches and rates of decomposition after two years. Analyses were carried out using the package nlme (Pinheiro et al. 2009) in R ver. 2.11.1 (R Core Development Team).

To test whether there were effects of inoculation treatments and rat invasion status on community structure, we used Anderson's (2001) non-parametric multivariate ANOVA in the R vegan package (Oksanen et al. 2008) using the β_{sim} metric of community dissimilarity (Koleff et al. 2003). Because the R implementation of non-parametric multivariate ANOVA (ADONIS) does not account for hierarchical data, we took a multi-step approach to analyzing treatment effects on fungal community structure. To determine whether community structure was significantly correlated with rates of decomposition we used the Mantel-test (Legendre and Legendre 1998) for the community dissimilarity matrix against a dissimilarity matrix of decomposition rates. To further examine the shape of the relationship between community structure and function we used quantile regression to compare the 5th, 50th and 95th quantiles for rat-free and rat-invaded islands using the R package, quantreg (Koenker 2011).

Results

Fungal community structure

Fungal community composition was significantly different between rat-free and rat-invaded islands ($r^2 = 0.05$, $F_{1,31} = 2.07$, $p = 0.008$, Fig. 1) and between the experimental branches and the sawdust used for the inoculation treatments ($r^2 = 0.15$, $F_{1,31} = 6.29$, $p = 0.001$). Inoculation treatments had no significant effect on final community structure in the experimental branches ($r^2 = 0.01$, $F_{2,\ 226} = 0.99$, $p = 0.31$) even though the inocula made from wood pieces collected on each island varied greatly in fungal OTU richness, ranging from 3 to 24 OTUs per inoculum. Observed fungal richness in the experimental branches ranged from 1 to 20 OTUs per branch and from 19 to 60 OTUs per island, but this variation was not explained by rat invasion status or inoculation treatments (Supplementary material Appendix A2, Model 1).

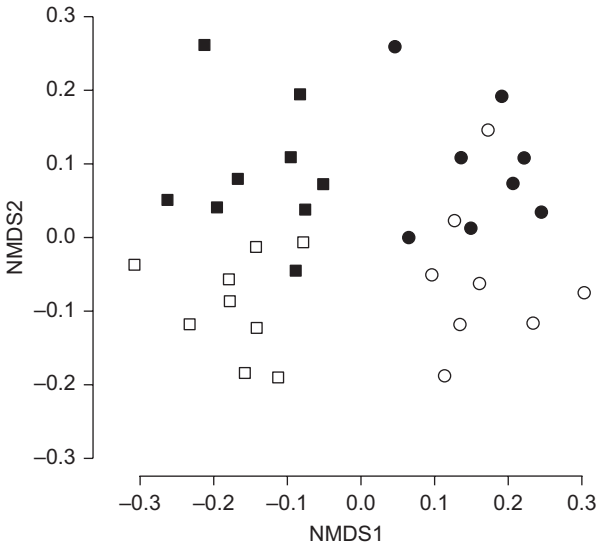

Figure 1. Rat status and substrate type significantly affected fungal community structure. The figure shows NMDS plot for fungal communities observed on different islands based on the β_{sim} metric of dissimilarity. Symbols depict different substrates (circles = initial sawdust inoculum, squares = harvested communities from experimental wood segments), and colors rat invasion status (black = rat-invaded, white = rat-free). Each data point includes all replicates from the single, pooled and no inoculation treatments. Differences between rat invasion and substrate type were significant based on non-parametric multivariate ANOVA ($p < 0.05$).

Wood decomposition rates

On average, experimental branches lost 51.3% (sd = 10.7%) of their mass over the two-year period of the experiment. Wood decomposition rates were not significantly affected by rat invasion status (Fig. 2), but decomposition was significantly slower in replicates with higher final OTU richness (Supplementary material Appendix A2 Model 2; Fig. 2) and slower in non-inoculated controls than in the replicates initially inoculated with fungi (Supplementary material Appendix A2 Model 2). There was a significant overall correlation between community structure and decomposition on rat-free islands (Mantel $r = 0.16$, $p = 0.003$, Fig. 3a), but not on rat-invaded islands (Mantel $r = 0.04$, $p = 0.12$, Fig. 3b), with no overlap in the 95% confidence intervals of the slopes for the two sets of islands (rat-free 95% CI = 0.12–0.19, rat-invaded 95% CI = 0.009–0.065). On rat-free islands, quantile regression detected a significant triangular distribution of data, with a progressively steeper slope moving from the 5% to the 95% quantiles (5% slope = 0.008, 50% slope = 0.08, 95% slope = 0.21). The triangular shape indicates that similar communities generally converged on similar rates of decomposition (e.g. the empty upper left corner of Fig. 3a shows that there are no identical communities with very different rates of decomposition), but that dissimilar communities were not necessarily different in decomposition rate. In contrast, on rat-invaded islands, there was less

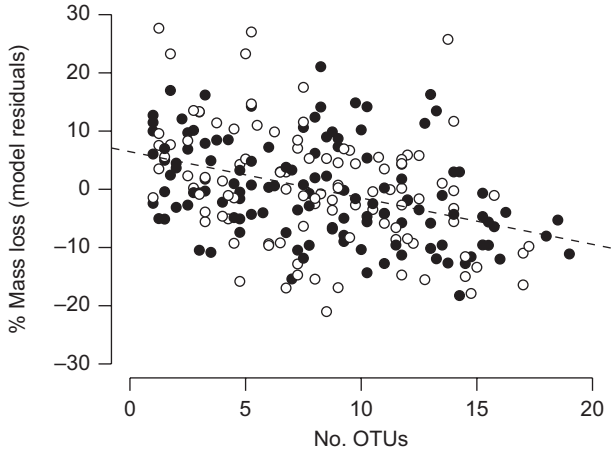

Figure 2. Decomposition rate decreased with increasing fungal richness. The figure shows partial linear regression of decomposition residuals against the number of fungal OTUs detected in individual logs after two years of field decomposition ($r^2 = 0.15$, $t = -6.217$, $p < 0.001$). The partial linear regression model included effects of log-transformed initial branch weight and inoculation treatments. There was no difference in the effect of fungal richness on decomposition rates between rat-free (white) and rat-invaded (black) islands.

variability in decomposition between dissimilar communities (empty upper right hand corner of Fig. 3b), and the relationship was correspondingly flat across the dataset (5% slope = 0.002, 50% slope = 0.03, 95% slope = 0.006).

Discussion

Our results indicate that rat invasion caused a predictable change in the structure of fungal wood-decomposing communities across independent island ecosystems (Fig. 1). Given the detection difficulties associated with fungi, the large number of fungal species, and the high degree of variability across samples in fungal species composition (Peay et al. 2008), our data indicates a profound reworking of fungal community structure as a resultof rat invasion. Whether this shift is related to physical changes in the environment (e.g. reduced bioturbation by seabirds, decreased marine-derived nitrogen levels in soil) or part of a biotic multi-trophic response to changes in other components of the soil food web (Fukami et al. 2006) is not clear yet. Nevertheless, because rats are unlikely to feed directly on wood-decomposing fungi (Caut et al. 2008), our results provide experimental evidence for an indirect effect of introduced animals on decomposer communities.

Furthermore, the relationship between fungal community similarity and wood mass-loss similarity also changed as a result of rat invasion. The potential links between soil community structure and function are well-documented (Kourtev et al. 2002, van der Putten et al. 2007, Hol et al. 2010). In this system, we found that on rat-free islands, there was a significant correlation between community distance and mass loss difference, with similar fungal communities tending to have similar amounts of wood mass

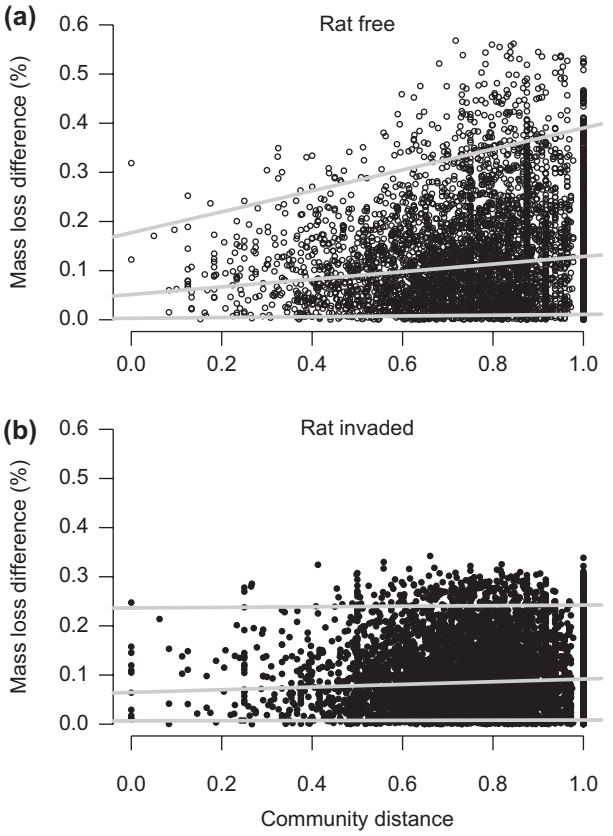

Figure 3. Relationships between fungal community similarity and decomposition rate similarity. The figure plots the difference in community structure against the difference in rates of decomposition for individual wood segments for (a) rat-free and (b) rat-invaded islands. The figure shows that on rat-free islands, different communities have highly variable rates of decomposition, whereas on rat-invaded islands, there is less variation in decomposition rates across communities. Lines are regression against the 5th, 50th and 95th quantile respectively from bottom to top. The change in slope from 5th to 95th reflects the triangular shape of the data.

loss (Fig. 3a). In contrast, on rat-invaded islands, there appeared to be less variation in function among communities (i.e. comparing the range of the y-axis in Fig. 3a vs 3b), perhaps suggesting functional simplification of the community. This type of functional homogenization by biological invasion has been identified as a major risk for invaded communities (Olden et al. 2004), but has not been shown in fungi until this study, to our knowledge.

The absence of a rat effect on overall decomposition rates (Fig. 2) despite the substantial changes in fungal community structure (Fig. 1) is seemingly inconsistent with the observed relationships between fungal community structure and wood decomposition rates (Fig. 2, 3, see also Toljander et al. 2006, Fukami et al. 2010). A previous study on the same islands found that decomposition of locally sourced leaf litter was slower on rat-invaded islands because rat invasion reduced leaf N content (Wardle et al. 2009). By using wood from a single tree, we experimentally eliminated one source of potential nutrient effects in this study. Thus, our results suggest that changes in fungal community

structure per se may not directly affect mean decomposition rates. Rather, decomposition in this system may be controlled more strongly by abiotic factors – directly affecting decomposition, indirectly influencing it via changes in fungal community structure, or perhaps most likely both.

In fact, dissimilar fungal communities (e.g. far right end of the x-axis of Fig. 3) often had nearly identical rates of decomposition on both rat-free and rat-invaded islands. This result may reflect one of two possible scenarios with respect to functional redundancy in fungal communities. First, community composition could be dominated by functionally unimportant (and thus redundant) taxa, while rates of decomposition could be driven by only a few key taxa that are shared by otherwise highly dissimilar communities (Jones et al. 1994, Aarssen 1997, Hooper and Vitousek 1997). Second, the regional pool of potential colonizers could contain many functionally important yet redundant taxa, a more classical functional redundancy scenario (Tilman et al. 1997, Yachi and Loreau 1999, Hooper et al. 2005). Discriminating between these two scenarios requires additional experimentation.

We also found that fungal richness was negatively correlated with rates of wood decomposition. While most studies tend to emphasize positive relationships between bio-diversity and ecosystem function (Tilman et al. 1997), other experimental studies with decomposers have also shown that decomposition is often slowest at the highest levels of diversity (Toljander et al. 2006, Fukami et al. 2010, Dickie et al. 2012). This negative effect of diversity is likely because wood-decomposing fungi are highly territorial (Cooke and Rayner 1984, Boddy 2000) and combative interactions consume more fungal resources in high diversity settings. This appears to be in contrast with degradation of simple sugars in leaf litter, which appear to decompose more rapidly with increasing fungal species richness (LeBauer 2010). While less is known about competition in litter decomposers, it seems likely that competitive interactions are less important in ephemeral resources.

The importance of priority effects and historical contingency on patterns of community assembly has been shown in several recent studies (Fukami et al. 2005, Chase 2010, Dickie et al. 2012), but in our investigation manipulation of initial community composition using inoculation treatments did not have strong effects on fungal community structure. It is possible that this lack of effect is due to failure of the inoculum treatments to produce strong variation in starting communities, given that there was no difference in species richness or community structure between the single versus pooled inoculum treatments. Furthermore, arrival mechanism can influence the outcome of fungal competition and colonization, and our use of ground wood for inoculation may not perfectly mirror the normal colonization process of woody substrates. Primary colonization of unoccupied wood may often be from fungal spores by species with weak competitive ability, which are eventually replaced by aggressive competitors colonizing from hyphal cords (Coates and Rayner 1985). Later arrivals may be superior competitors in part because hyphae growing out from other colonized substrates have access to large resource pools they can invest in secondary resource capture (Holmer and Stenlid 1993, 1997). Inoculation with ground wood may thus have introduced weak competitors with small inocula bases. However, as we used the same treatments on rat-invaded and rat-free islands, this should not have led to any bias in our results. The fact that community composition converged in inoculated and non-inoculated controls suggests that the strong successional patterns frequently observed in woody substrates (Frankland 1998) may have obscured the inoculum treatment effects over the two-year period of the study. Our results suggest that local-scale variation in starting conditions may sometimes have small effects on fungal community development relative to larger-scale perturbations, such as the impacts of invasive animals.

Conclusions

It is becoming clear that the effects of introduced animals can extend far beyond the direct consumption of prey (O'Dowd et al. 2003, Croll et al. 2005). In this study, we have provided the first evidence, to our knowledge, that the indirect effects of animal invasion can extend to the structure of wood-decomposing fungal communities, but not necessarily their overall function. If this is the case, removing rats from the islands could reverse rat-induced changes in the relationship between the structure and function of fungal communities. However, our results also indicate that even in cases where no obvious change in function is evident, changes in community structure may occur and that there may be shifts in the relationship between community structure and function. Most previous studies of decomposer responses to animals have used coarse metrics of community structure, such as gross biomass, phospholipid fatty acids and total respiration (Mikola and Setälä 1998, Wardle et al. 2001, Fukami et al. 2006). Indirect effects of introduced animals on decomposer community structure may be more widespread than generally suspected.

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Supplementary material (available online as Appendix O20813 at <www.oikosoffice.lu.se/appendix>). Appendix A1.