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LETTERS

Effects of species and functional group loss on island ecosystem properties

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Considerable recent attention has focused on predicting how the losses of species and functional groups influence ecosystem properties[1,2], but the extent to which these effects vary among ecosystems remains poorly understood[3,4]. Island systems have considerable scope for studying how biotic and abiotic factors influence processes in different ecosystems, because they enable the simultaneous study of large numbers of independent replicate systems at ecologically meaningful spatial scales[5–7]. We studied a group of 30 islands in northern Sweden, for which island size determined disturbance history, and therefore vegetation successional stage and biotic and abiotic ecosystem properties. On each island we conducted a seven-year study that involved experimental removals of combinations of both plant functional groups and plant species. We show that although losses of functional groups and species often impaired key ecosystem processes, these effects were highly context-dependent and strongly influenced by island size. Our study provides evidence that the consequences of biotic loss for ecosystem functioning vary greatly among ecosystems and depend on the specific abiotic and biotic attributes of the system.

The recent interest in understanding how losses of biota from real ecosystems influence ecosystem processes has resulted in a significant and growing number of studies, some of which have suggested that biodiversity is a major driver of ecosystem properties[4,8,9] and others of which have not[10–12]. The interpretations of many of these studies have been hotly debated[1,2]. However, it seems likely that discrepancies between the results of different studies are attributable in large part to the differences in context between studies. For example, whether or not ecosystem properties and functions are responsive to diversity can depend on soil nutrient availability[3], temporal factors[13], the type of ecosystem functions considered[2], trophic interactions[14] and spatial scale[1]. However, definite empirical evidence for such context dependence in real ecosystems is scarce.

In this study, we used a group of 30 forested islands in two adjacent lakes in northern Sweden, Lake Uddjaure and Lake Hornavan (65° 55′ N to 66° 09′ N and 17° 43′ E to 17° 55′ E), to compare how contrasting ecosystems respond to losses of plant functional groups and species. For these islands, the primary driver of ecosystem properties is disturbance regime: large islands burn more often than smaller ones because they have a larger area that can be intercepted by lightning strikes[11]. This creates a successional gradient across islands; large islands that are early-successional support plant species that grow faster, support more biomass and produce litter of higher quality than do smaller islands[11,15]. This in turn affects ecosystem properties, with smaller islands supporting less productivity, lower rates of nutrient cycling, and lower supply rates of available soil nutrients compared with larger islands[11,15]. This system offers potential for studying how interactions between resident biota and the current state of physical and chemical properties can affect ecosystem properties. We studied 30 islands, which include ten in each of three size classes known to differ markedly in successional age and therefore in biotic and abiotic factors; these classes are 'large' (>1.0 ha), 'medium' (0.1–1.0 ha) and 'small' (<0.1 ha)[15].

Table 1 | Effects of plant functional group removal, island size and two-way interactions on above- and belowground properties

	Response variable*									
	R	*S*	*M*	*A*	*R* × *S*	*R* × *M*	*S* × *M*	*R* × *A*	*S* × *A*	*M* × *A*
Total shrub cover	**6.5 (0.011)**	–	0.6 (0.446)	**4.3 (0.015)**	–	0.2 (0.701)	–	1.7 (0.185)	–	0.0 (0.975)
Moss biomass	0.3 (0.867)	0.1 (0.723)	–	**3.7 (0.028)**	0.3 (0.563)	–	–	0.0 (0.970)	0.2 (0.814)	–
BR	**27.5 (<0.001)**	**15.6 (<0.001)**	0.9 (0.347)	**10.0 (<0.001)**	3.2 (0.074)	0.2 (0.678)	0.7 (0.405)	**4.5 (0.010)**	**8.7 (<0.001)**	0.2 (0.845)
SIR	**8.3 (0.004)**	**19.2 (<0.001)**	0.1 (0.825)	**23.0 (<0.001)**	0.1 (0.715)	0.0 (0.918)	0.2 (0.704)	0.1 (0.917)	**6.9 (0.001)**	0.4 (0.678)
[Mineral N]†	1.7 (0.191)	**32.6 (<0.001)**	1.8 (0.183)	**16.8 (<0.001)**	0.0 (0.923)	0.1 (0.705)	2.1 (0.149)	0.1 (0.931)	**11.2 (<0.001)**	1.0 (0.372)
DON†	**8.3 (0.004)**	0.0 (0.891)	0.6 (0.427)	**4.7 (0.009)**	0.0 (0.993)	1.2 (0.285)	0.4 (0.551)	**3.0 (0.049)**	0.1 (0.940)	0.1 (0.921)
N ratio	**3.2 (0.074)**	**12.1 (<0.001)**	0.4 (0.534)	**7.0 (0.001)**	0.2 (0.647)	0.8 (0.367)	3.1 (0.078)	**3.4 (0.037)**	**4.9 (0.009)**	0.2 (0.815)
Decomposition rate	**8.2 (0.005)**	**32.8 (<0.001)**	0.9 (0.343)	**9.4 (<0.001)**	3.5 (0.061)	1.2 (0.285)	0.6 (0.809)	**7.9 (<0.001)**	**6.9 (0.001)**	1.5 (0.212)
MANOVA‡	**6.2 (<0.001)**	**18.0 (<0.001)**	1.5 (0.166)	**10.0 (<0.001)**	1.7 (0.119)	0.5 (0.814)	0.9 (0.478)	**2.9 (0.001)**	**5.6 (<0.001)**	0.5 (0.898)

F values (with *P* values in parentheses) from univariate ANOVA and MANOVA are presented for effects of plant functional group removal, island size and two-way interactions, after seven years. Statistically significant values (at $P = 0.05$) are shown in bold.
*Factors are: *R*, tree root removal; *S*, shrub removal; *M*, moss removal; *A*, island area class. Results are from three-way univariate ANOVAs for aboveground variables and four-way univariate ANOVAs and MANOVA for belowground variables. Results for three- and four-way interaction terms were rarely statistically significant and are therefore not presented. The degrees of freedom for *R*, *M*, *S* and all interactions among them are 1 for univariate ANOVAs and 6 for MANOVA. For *A* and all interactions involving *A*, there are 2 degrees of freedom for univariate ANOVAs and 12 for MANOVA. Residual degrees of freedom are 108, 216 and 211 for aboveground ANOVAs, belowground univariate ANOVAs and MANOVA, respectively.
BR, basal respiration; SIR, substrate-induced respiration; DON, dissolved organic nitrogen; N ratio = (mineral N)/(mineral N + DON).
†Analyses done on (log + 1)-transformed data.
‡*F* values estimated from Wilk's lambda.

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We used a 'removal experiment' approach, because this is a powerful tool for investigating the effects of local, non-random losses of biotic components and species interactions in natural ecosystems[16]. Fourteen plots, each representing a different removal treatment, were established on each island in August 1996 (420 plots in total). The following removal treatments were performed: a full factorial combination of three plant functional group removals (removal of tree roots by root trenching, ericaceous dwarf shrub removal, and moss removal), and a full factorial combination of three ericaceous dwarf shrub species removals (removal of *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum*) (see Methods). This design allows assessment of the contributions of all possible interactions among functional groups and among major species within a functional group to ecosystem functioning at local spatial scales across the island size gradient. Here we report on measures of aboveground and belowground ecosystem performance seven years after initiation of the study.

Measures of the cover of each shrub species made on each plot after seven years showed that total shrub cover was unaffected by moss removal (Table 1), but was reduced by an average of 9.9% by root trenching; the magnitude of this effect was independent of island size (Table 1). There was a much stronger influence of shrub species removals on total shrub cover (Table 2 and Fig. 1); all single species removals, and all two-way combinations of removals, had negative effects. This means that at the within-island scale there is a distinct positive relationship between plant diversity and biomass. This is indicative of resource partitioning or resource use complementarity among coexisting species[1,2,13]. However, this partitioning is only partial; for five out of six cases a given species also showed a positive overall response to the removal of another species (Table 2). Across all the islands, *V. myrtillus* was enhanced by 31.1% and 26.0% by the removal of *V. vitis-idaea* and *E. hermaphroditum*, respectively. *V. vitis-idaea* was enhanced by 19.1% by the removal of *V. myrtillus*, but was unaffected by removal of *E. hermaphroditum*. *E. hermaphroditum* was enhanced by 31.9% and 80.6% by the removal of *V. myrtillus* and *V. vitis-idaea*, respectively. This indicates that after seven years, species have at least partially compensated for removal of other species of the same functional group.

In most cases, the magnitude of the effect on one species of removing another species did not differ significantly across island size classes (Table 2), meaning that the relative balance between resource use complementarity and compensatory effects was not context-dependent. In contrast, the effects on total plant cover of removing two of the three species were significantly influenced by island size class (Table 2 and Fig. 1). Specifically, effects of removing *V. myrtillus* on total cover were strongest on medium and large islands, but removal of *E. hermaphroditum* had the strongest effects on small islands. As the biomass of *V. mytrillus* is greatest on large islands, and *E. hermaphroditum* biomass is maximal on small islands, these results emphasize that within any given ecosystem, effects of species loss are greatest when dominant species are involved[17], and that context-dependent effects of species removals across ecosystems can arise whenever different species dominate in different ecosystems. These effects remained significant after the amount of vegetation removed from each plot at the start of the study was accounted for as a covariate (see Supplementary Information), presumably because the remaining species had at least partially compensated for those species that were removed.

Because the aboveground and belowground subsystems interact to regulate community and ecosystem properties[18], we also assessed a suite of functionally relevant belowground properties for each plot. We found that removals of each of two functional groups (tree roots and shrubs) and each of two species (*V. myrtillus* and *V. vitis-idaea*) influenced several of the measured properties (Tables 1, 2 and Fig. 2). Wherever they had significant effects, these four removals each reduced soil microbial respiration, substrate-induced respiration (SIR; a surrogate for microbial biomass) and litter decomposition rates, and increased the amount of available mineral nitrogen and the ratio of mineral nitrogen to dissolved organic nitrogen (Fig. 2). Collectively, the trees and two *Vaccinium* species account for the majority of net primary productivity (NPP) on the islands[15], and the removal of these components would serve to reduce NPP, in turn inducing bottom-up limitation of the soil microbial biomass, depressing microbial activity, and impairing functions performed by the microflora, such as decomposition[18]. Reduced uptake of nitrogen by plants and microbes after these removals would explain

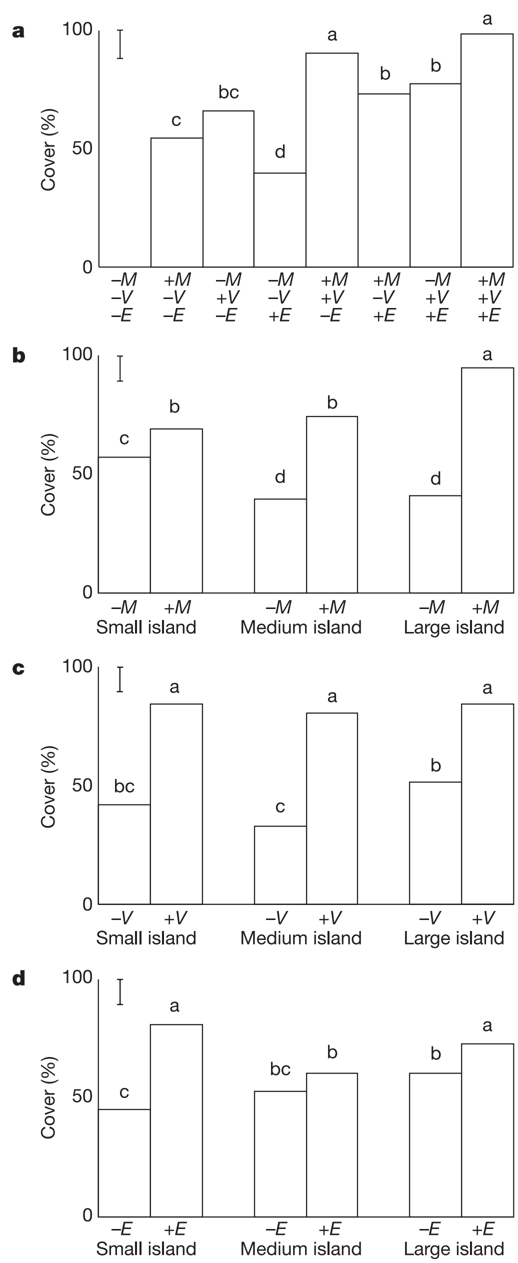

Figure 1 | The influence of shrub species removals on total shrub cover in island ecosystems. a–d, Effects of interactions between different shrub species removal treatments (**a**), and between island size and removals of *V. myrtillus* (**b**), *V. vitis-idaea* (**c**) and *E. hermaphroditum* (**d**) on total shrub cover after seven years, measured as total number intercepts per 100 points. Removal treatment codes are: *V. myrtillus* removed ($-M$) or not removed ($+M$); *V. vitis-idaea* removed ($-V$) or not removed ($+V$); *E. hermaphroditum* removed ($-E$) or not removed ($+E$). Within each panel, bars topped by the same letter (a, b, c or d) are not significantly different at $P = 0.05$ (least significant difference (LSD) test), and vertical bars represent LSD values at $P = 0.05$.

the greater amounts of mineral nitrogen present.

Notably, there were significant interactive effects between these removal treatments and island size on belowground properties (Tables 1 and 2), which remained significant when the amount of shrub biomass removed at the start of the study was included as a covariate (see Supplementary Information). Specifically, these removals frequently had significant effects on large and medium sized islands, but never on small ones (Fig. 2). The interactive effects of the two *Vaccinium* species with island size probably emerge because the densities of these species themselves vary across the island size gradient[11,15]. These species are relatively productive[15], show a high turnover of tissue (see Supplementary Table 1) and produce litter of a relatively high quality[19], which should in turn promote soil biota[19]. Therefore, removal of these species should exert greater bottom-up regulation on the soil biota on the islands that they dominate. In contrast, *E. hermaphroditum*, which dominates on small islands, is less productive and produces poorer quality litter that is well defended; loss of this species from islands is therefore less likely to impair decomposer organisms and processes[19]. In combination, these results show that belowground effects of losses of biota at either the functional group or species level are context-dependent, and are affected by which species are lost, and the ecosystems that they are lost from.

This study also highlights the importance of spatial scale. It has frequently been suggested that discrepancies across studies on how biodiversity affects ecosystem properties are influenced in part by differences in scale, and that studies at the across-ecosystem scale (representing most observational studies) can yield different results to those at the within-ecosystem scale (representing most experimental studies)[4,18,20]. Island systems, in which each island operates as an unambiguously separate ecosystem, have the potential to serve as powerful tests of this idea. Earlier studies on this system have shown that at the across-ecosystem (between island) scale, most ecosystem processes were negatively related to plant diversity, because possible effects of diversity were entirely overridden by plant compositional effects or extrinsic abiotic factors[5,11,15]. Here we show that at the within-island scale, richness of species in the shrub layer (but not of functional groups) consistently positively affected total shrub cover (and therefore biomass) across the entire island size gradient. Because of the fully factorial nature of the experiment (made possible by the low floristic diversity of the system), these results cannot be explained by statistical artefact, an issue that has created much debate regarding earlier studies[1,2,18]. These within-island, aboveground effects of plant diversity did not translate consistently belowground: although removal of some biotic components affected soil properties on large islands, this never occurred on small islands. However, whenever removals of species or functional groups influenced key soil processes (respiration or decomposition) within islands, the effects were always negative, indicating the opposite direction of relationship between diversity and function to that observed across islands.

These results have several implications. First, they point to the utility of islands for investigating questions about community and ecosystem ecology. Abiotic and biotic attributes that vary among islands do not just determine the types of communities present[21–23], but also how these communities determine ecosystem-level attributes, and in particular what happens to ecosystem functioning when components of island biotas are lost. Second, they show, through the use of independent replicated ecosystems, that components of biodiversity can promote ecosystem process rates within

Table 2 | Effects of shrub species removal, island size and two-way interactions on above- and belowground properties

	Response variable*			
	M	*V*	*E*	*A*
Total shrub cover	**119.8 (<0.001)**	**180.9 (<0.001)**	**40.5 (<0.001)**	**4.3 (0.015)**
V. myrtillus cover	–	**5.9 (0.017)**	**3.8 (0.049)**	**37.3 (<0.001)**
V. vitis-idaea cover	**4.4 (0.039)**	–	1.6 (0.205)	**6.1 (0.003)**
E. hermaphtoditum cover	**3.7 (0.050)**	**17.3 (<0.001)**	–	**41.9 (<0.001)**
Moss biomass	0.2 (0.669)	1.6 (0.214)	0.1 (0.708)	1.3 (0.276)
BR	0.9 (0.334)	**25.3 (<0.001)**	0.2 (0.621)	**23.6 (<0.001)**
SIR	0.2 (0.664)	**17.0 (<0.001)**	0.1 (0.739)	**12.3 (<0.001)**
Mineral N concn†	**6.4 (0.012)**	**10.5 (0.001)**	0.8 (0.370)	**13.9 (<0.001)**
DON†	0.3 (0.581)	0.1 (0.936)	0.2 (0.636)	**3.6 (0.028)**
N ratio	0.8 (0.359)	**5.7 (0.018)**	0.2 (0.689)	1.3 (0.271)
Decomposition rate	**14.1 (<0.001)**	**13.8 (<0.001)**	0.6 (0.455)	**20.2 (<0.001)**
MANOVA‡	**5.3 (<0.001)**	**12.0 (<0.001)**	0.3 (0.917)	**8.4 (<0.001)**

	Response variable*					
	M × *V*	*M* × *E*	*V* × *E*	*M* × *A*	*V* × *A*	*E* × *A*
Total shrub cover	**11.9 (<0.001)**	**3.9 (0.049)**	**9.8 (0.002)**	**15.5 (<0.001)**	2.1 (0.129)	**7.6 (<0.001)**
V. myrtillus cover	–	–	0.4 (0.545)	–	1.0 (0.388)	0.3 (0.712)
V. vitis-idaea cover	–	1.2 (0.285)	–	1.6 (0.218)	–	**4.4 (0.014)**
E. hermaphtoditum cover	0.1 (0.825)	–	–	0.8 (0.471)	0.6 (0.573)	–
Moss biomass	3.9 (0.051)	1.0 (0.323)	1.3 (0.226)	0.7 (0.505)	0.3 (0.709)	0.3 (0.773)
BR	0.2 (0.886)	**5.7 (0.018)**	0.5 (0.468)	0.7 (0.484)	**7.1 (0.001)**	0.1 (0.917)
SIR	2.2 (0.139)	0.0 (0.910)	0.1 (0.722)	0.5 (0.615)	**5.2 (0.006)**	0.2 (0.843)
Mineral N concn†	2.0 (0.163)	0.9 (0.340)	0.6 (0.429)	**3.1 (0.045)**	**4.1 (0.018)**	1.0 (0.361)
DON†	0.1 (0.830)	0.1 (0.765)	0.7 (0.657)	0.9 (0.425)	0.0 (0.983)	0.2 (0.835)
N ratio	0.5 (0.482)	0.8 (0.388)	0.1 (0.736)	0.4 (0.645)	1.9 (0.147)	0.6 (0.574)
Decomposition rate	**5.1 (0.025)**	**8.4 (0.004)**	3.5 (0.064)	**3.7 (0.026)**	**4.4 (0.014)**	0.7 (0.477)
MANOVA‡	1.5 (0.166)	**3.1 (0.006)**	0.7 (0.646)	**1.8 (0.044)**	**4.4 (<0.001)**	0.6 (0.831)

F values (with *P* values in parentheses) from univariate ANOVA and MANOVA are presented for effects of shrub species removal, island size and two-way interactions on above- and belowground properties after seven years. Statistically significant values (at $P = 0.05$) are shown in bold.

*Factors are: *M*, *V. myrtillus* removal; *V*, *V. vitis-idaea* removal; *E*, *E. hermaphroditum* removal; *A*, island area class. Results are from three-way univariate ANOVAs for responses of individual species and four-way ANOVA and MANOVA for all other data. The MANOVA incorporates all belowground variables. Results for three- and four-way interaction terms were rarely statistically significant and are not presented. The degrees of freedom for *M*, *V*, *E* and all interactions among them are 1 for univariate ANOVAs and 6 for MANOVA. For *A* and all interactions involving *A*, there are 2 degrees of freedom for univariate ANOVAs and 12 for MANOVA. Residual degrees of freedom are 108 for responses of individual species, 216 for univariate ANOVAs on all other response variables, and 211 for MANOVA.

BR, basal respiration; SIR, substrate-induced respiration; DON, dissolved organic nitrogen; N ratio = (mineral N)/(mineral N + DON).

†Analyses done on (log + 1)-transformed data.

‡*F* values estimated from Wilk's lambda.

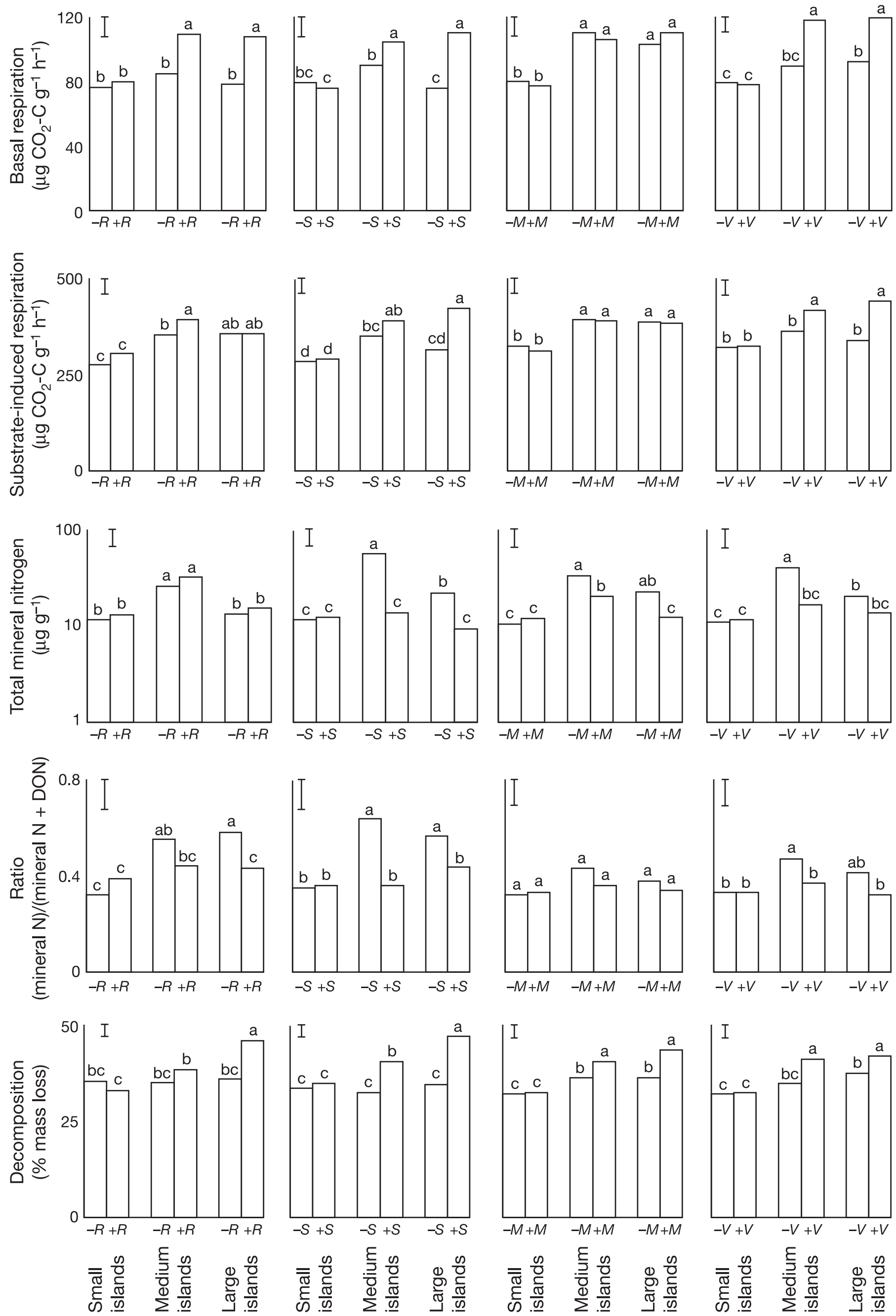

Figure 2 | Interactive effects of island size and removals of functional groups or species on selected belowground properties after seven years. Removal treatments shown are: tree roots removed ($-R$) or not removed ($+R$), all shrubs removed ($-S$) or not removed ($+S$), *Vaccinium myrtillus* removed ($-M$) or not removed ($+M$), and *Vaccinium vitis-idaea* removed ($-V$) or not removed ($+V$). Data for removal of mosses or of *E. hermaphroditum* are not shown as these treatments did not interact with island size to affect the response variables. DON, dissolved organic nitrogen. Within each panel, bars topped by the same letter (a, b or c) are not significantly different at $P = 0.05$ (LSD test), and vertical bars represent LSD values at $P = 0.05$.

ecosystems, even when biodiversity and process rates are negatively correlated across ecosystems. Finally, they show that the effects of losses of subsets of the resident biota depend on which ecosystems are considered; removals of particular functional groups or species were found to have important effects on some islands but not others, depending on island size and therefore historical disturbance regime and successional stage. This provides evidence that the effects of species and functional groups on ecosystem properties are highly context-dependent, and indicates that seemingly idiosyncratic biodiversity effects can be better understood through comparisons of independent ecosystems that differ in fundamental abiotic and biotic properties.

METHODS

Plot and treatment setup. We established 14 experimental plots on each of the 30 islands, each representing a different removal treatment of functional groups or species. The experiment was conducted as two components. For the 'functional group removal' component, this consisted of a full factorial combination of three factors (eight treatments in total): tree root removal, ericaceous dwarf shrub removal and moss removal. For the 'species removal' component, this also consisted of a full factorial combination of three factors (eight treatments in total): removal of *Vaccinium myrtillus*, removal of *Vaccinium vitis-idaea* and removal of *Empetrum hermaphroditum*. These shrubs dominate the ericaceous shrub layer in large, medium and small islands, respectively[11,15]. Two treatment plots (no removals and removal of all shrubs) were common to both components of the study, yielding 14 plots per island. The three manipulated functional groups represent >99% of all plant biomass present, and the three manipulated shrub species collectively represent 98% of total biomass in the dwarf shrub layer. All plots were 55 cm × 55 cm, but only the inner 45 cm × 45 cm were ever measured or sampled. All plots were located at similar distances from the shore for each island, regardless of island size, to prevent edge and microclimatic effects from confounding the results[11,15]. These plots are in the vicinity of plots used for other studies previously performed on these islands[15].

The experiment was established in August 1996 (when each treatment was implemented for the first time) and has been maintained annually ever since. Tree root removals have been performed by annual root trenching to below the tree rooting zone[24], and dwarf shrub and moss manipulation treatments have been conducted through annual physical removal of vegetation[16]. It is recognized that both root trenching and vegetation removals impose initial disturbance effects, but these are likely to be transient[16,24] and of minimal importance by year seven. Notably, the relative effects of different treatments on vegetation cover performed in these plots varied little after year four. Removal of tree effects was only performed belowground. However, the proportion of total incoming light intercepted by trees (measured on each island in August 2001)[15] is low and therefore unlikely to be sufficient to impair understory vegetation.

Measurements. Every August from 1996 until 2003, the total cover of each ericaceous dwarf shrub species was assessed in each plot by point quadrant analysis, by determining the total number of times the vegetation of that species was intercepted by a total of 100 downwardly projecting points[15]. For each of the three species, the total number of point intercepts is very closely correlated with aboveground standing biomass, with R^2 values consistently above 0.90 (ref. 15).

In August 2001, two nylon mesh litterbags (hole size 1.0 × 0.1 mm) were placed in each plot, and buried under about 3 cm of humus. Each litterbag contained 1.5 g of a standardised substrate: locally collected *Salix caprea* leaf litter (0.56% nitrogen, 21% lignin). Litterbags were left in the plots for two years and harvested in August 2003. At that time, dry weight was determined by drying at 80 °C for 24 h.

Soil samples were collected in August 2003. For each plot, three separate soil samples were collected to 5-cm humus depth, bulked within the plot, and sieved to 4 mm. Total nitrogen, phosphorous, ammonium, nitrate and dissolved organic nitrogen (DON) concentrations were measured using automated colourimetric procedures[25]. Soil basal respiration and substrate-induced respiration (a relative measure of active microbial biomass) were assessed *in vitro* through the use of infrared gas analysis[26,27].

Data for all response variables for aboveground variables were analysed by univariate analysis of variance (ANOVA). Belowground variables (for which the same ANOVA model could be applied to all response variables) were analysed by multivariate ANOVA (MANOVA) followed by univariate ANOVAs for each variable. Separate analyses were performed for the functional group removal and species removal components of the study. For each analysis, island size class and removals of each of the species or functional groups were fixed effects, and individual islands served as the units of replication. Data was transformed as necessary to satisfy assumptions of ANOVA and MANOVA.

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1. Loreau, M. *et al.* Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294,** 804–808 (2001).
2. Hooper, D. U. *et al.* Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. *Ecol. Monogr.* **75,** 3–35 (2005).
3. Fridley, J. D. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia* **132,** 271–277 (2002).
4. Hector, A. *et al.* Plant diversity and productivity experiments in European grasslands. *Science* **286,** 1123–1126 (1999).
5. Wardle, D. A. Islands as model systems for understanding how species affect ecosystem properties. *J. Biogeogr.* **29,** 583–592 (2002).
6. Vitousek, P. M. Oceanic islands as model systems for ecological studies. *J. Biogeogr.* **29,** 573–582 (2002).
7. Anderson, W. B. & Polis, G. A. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia* **118,** 324–332 (1999).
8. Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H. & Woodfin, R. M. Declining biodiversity can alter the performance of ecosystems. *Nature* **368,** 734–737 (1994).
9. Tilman, D. *et al.* Diversity and productivity in a long-term grassland experiment. *Science* **294,** 843–845 (2001).
10. Hooper, D. U. & Vitousek, P. M. The effects of plant composition and diversity on ecosystem processes. *Science* **277,** 1302–1305 (1997).
11. Wardle, D. A., Zackrisson, O., Hörnberg, G. & Gallet, C. Influence of island area on ecosystem properties. *Science* **277,** 1296–1299 (1997).
12. Enquist, B. J. & Niklaus, K. J. Invariant scaling relations across tree-dominated communities. *Nature* **410,** 655–660 (2001).
13. Hooper, D. U. & Dukes, D. S. Overyielding among plant functional groups in a long-term experiment. *Ecol. Lett.* **7,** 95–105 (2004).
14. Mulder, C. P. H., Koricheva, J., Huss-Danell, K., Högberg, P. & Joshi, J. Insects affect relationships between plant species richness and ecosystem processes. *Ecol. Lett.* **2,** 237–246 (1999).
15. Wardle, D. A., Hörnberg, G., Zackrisson, O., Kalela-Brundin, M. & Coomes, D. A. Long term effects of wildfire on ecosystem properties across an island area gradient. *Science* **300,** 972–975 (2003).
16. Díaz, S., Chapin, F. S. III, Symstad, A., Wardle, D. A. & Huennecke, L. Functional diversity revealed through removal experiments. *Trends Ecol. Evol.* **18,** 140–146 (2003).
17. Grime, J. P. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* **86,** 902–910 (1998).
18. Wardle, D. A. *Communities and Ecosystems: Linking the Aboveground and Belowground Components* (Princeton Univ. Press, Princeton, 2002).
19. Wardle, D. A., Nilsson, M.-C., Zackrisson, O. & Gallet, C. An ecosystem level perspective of allelopathy. *Biol. Rev.* **73,** 305–319 (1998).
20. Schmid, B. The species richness–productivity controversy. *Trends Ecol. Evol.* **17,** 113–114 (2002).
21. Gonzalez, A. & Chaneton, E. J. Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. *J. Anim. Ecol.* **71,** 594–602 (2002).
22. Spiller, D. A. & Schoener, T. W. Folivory on islands with and without insectivorous lizards: an eight-year study. *Oikos* **78,** 15–22 (1997).
23. Tscharntke, T., Steffan-Deweter, I., Kruess, A. & Thies, C. The contribution of small habitat fragments to the conservation of insect communities of grassland-cropland landscape mosaics. *Ecol. Appl.* **12,** 354–363 (2002).
24. Coomes, D. A. & Grubb, P. J. Impacts of root competition in forests and woodlands: a theorical framework and review of experiments. *Ecol. Monogr.* **70,** 171–207 (2000).
25. Technicon Instruments. *Individual/Simultaneous Determination of Nitrogen and/or Phosphorus in BD Acid Digests* (Technicon Industrial Systems, Tarrytown, 1997).
26. Anderson, J. P. E. & Domsch, K. H. A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biol. Biochem.* **10,** 215–221 (1978).
27. Wardle, D. A. Changes in the microbial biomass and metabolic quotient during leaf litter succession in some New Zealand forest and scrubland ecosystems. *Funct. Ecol.* **7,** 346–355 (1993).

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