Nitrogen niches revealed through species and functional group removal in a boreal shrub community

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Abstract. Most theories attempting to explain the coexistence of species in local communities make fundamental assumptions regarding whether neighbors exhibit competitive, neutral, or positive resource–use interactions; however, few long-term data from naturally assembled plant communities exist to test these assumptions. We utilized a 13-year experiment consisting of factorial removal of three shrub species (*Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*) and factorial removal of two functional groups (tree roots and feather mosses) to assess how neighbors affect N acquisition and growth of each of the three shrub species. The removal plots were established on each of 30 lake islands in northern Sweden that form a natural gradient of resource availability. We tested the hypotheses that: (1) the presence of functionally similar neighbors would reduce shrub N acquisition through competition for a shared N resource; (2) the removal of functional groups would affect shrub N acquisition by altering the breadth of their niches; and (3) soil fertility would influence the effects of neighbor removals. We found that the removal of functionally similar neighbors (i.e., other shrub species) usually resulted in higher biomass and biomass N, with the strength of these effects varying strongly with site fertility. Shrub species removals never resulted in altered stable N isotope ratios (δ^{15}N), suggesting that the niche breadth of the three shrubs was unaffected by the presence of neighboring shrub species. In the functional group removal experiment, we found positive effects of feather moss removal on *V. myrtillus* biomass and biomass N, and negative effects on *E. hermaphrotium* N concentration and *V. vitis-idaea* biomass and biomass N. Tree root removal also caused a significant shift in foliar δ^{15}N of *V. myrtillus* and altered the δ^{15}N, biomass, and biomass N of *E. hermaphroditum*. Collectively, these results show that the resource acquisition and niche breadth of the three shrub species are often affected by neighbors, and further that both the identity of neighbors and site fertility strongly determine whether these interactions are positive, negative, or neutral. These findings have implications for understanding species coexistence and the reciprocal relationships between productivity and species diversity in this ecosystem.

Key words: boreal shrubs; diversity theory; niche breadth; niche plasticity; northern Sweden; plant competition; removal experiment; resource use complementarity; species coexistence; stable N isotope ratio.

Introduction

A major focus in community ecology is to understand how plant species stably coexist in local communities (Hutchinson 1959, Tilman 1994, Hubbell 2001). Classical community theory predicts that stable coexistence should only occur if species occupy different resource niches (i.e., resource–use complementarity; Gause 1934, Hutchinson 1959), whereas several subsequent diversity theories assume the presence of resource competition and invoke alternative mechanisms for species coexistence in communities (e.g., Grime 1973, Connell 1978, Huston 1979, Rees 1993, Tilman and Pacala 1993, Tilman 1994, Chesson 2000, Hubbell 2001, Snyder 2008,

Wright et al. 2010). Despite key assumptions regarding plant niches in both classic and more recent diversity theories, long-term experimental field studies identifying plant niche relationships remain relatively scarce (Silvertown 2004, Ashton et al. 2010). Within the last decade there has been a resurgent interest in identifying resource-based plant niches, particularly in cold-climate ecosystems, where nitrogen (N) is often considered to be the primary limiting resource (Tamm 1991, Vitousek and Howarth 1991). These studies have aimed at understanding whether neighboring plant community members partition their use of different forms of available N (e.g., McKane et al. 2002, Nordin et al. 2004, Miller et al. 2007, Ashton et al. 2010), which has been proposed as a mechanism for species coexistence (McKane et al. 2002, Miller and Bowman 2002).

One approach that has been used to investigate the presence of different N niches is to supply naturally assembled plant communities different forms of ^{15}N-labeled soluble N substrates (i.e., NO_3^--N, NH_4^+-N,

amino acids, or peptides) to determine if preferential uptake of specific N forms by specific species occurs (e.g., McKane et al. 2002, Miller and Bowman 2002, Nordin et al. 2004, Harrison et al. 2007, Ashton et al. 2010). Although these studies have yielded substantial knowledge about N niches in natural plant communities, this approach is limited to relatively simple labeled-N substrates, results in artificially elevated soil N availability, and provides only a short-term perspective. These limitations are significant, given that the rate-limiting step in the N cycle in cold climate ecosystems is the depolymerization of complex organic N (Schimel and Bennett 2004), which controls the supply rate of simple organic and inorganic N substrates to plants. Plants are known to employ a range of strategies to acquire N from other N pools not considered in most labeling studies, such as acquisition of complex organic N through rhizosphere priming (Dijkstra et al. 2009), association with specific mycorrhizal functional groups (Bending and Read 1996, Schimel and Bennett 2004, Joanisse et al. 2008, 2009), and directly accessing newly fixed N from associative or free-living N-fixers (Granhall and Lindberg 1978, Gundale et al. 2010). This highlights that plant N niches are probably more complex than those revealed by the short-term uptake of simple soluble N substrates used in most isotope-labeling experiments, and that in the long term, competition or complementarity between species may involve a wide range of N uptake and acquisition pathways and processes.

An alternative approach to understanding whether resource–use complementarity or competition occurs within plant communities is to use a species removal experiment, combined with N accounting and analysis of ^{15}N natural abundance. Species removal experiments are powerful tools to understand how species interact in naturally assembled communities (Díaz et al. 2003, Silvertown 2004). In these experiments, a positive growth response to neighbor removal indicates resource competition, and no response suggests resource–use complementarity (Díaz and Cabido 1997, Suding et al. 2006, Bret-Harte et al. 2008). When combined with nutrient accounting and stable N isotope analysis, removal experiments can reveal over the long term whether the quantity of N acquired by the plant or the pathway or processes involved in acquisition are affected by neighbors, thereby revealing the relative niche space of coexisting species. Nitrogen stable isotope ratios (i.e., δ^{15}N) have been used to assess many N cycling processes known to influence plant N acquisition, such as ecosystem N inputs (i.e., biological N fixation or precipitation), N turnover (i.e., N mineralization and nitrification), and ecosystem N losses (i.e., gaseous or hydrological) (Evans 2007). Nitrogen isotopic signatures (δ^{15}N) vary among different ecosystem N pools as a result of discrimination of the heavier N isotope (^{15}N) during physical, chemical, and biological transformations (Evans 2007). As such, it is well known that plant δ^{15}N values are influenced by long-term soil N inputs and losses (Vitousek 2004, Compton et al. 2007),

the form of N acquired by the plant (organic N, NH_4^+-N, or NO_3^--N) (Evans 2007), as well as fractionation during mycorrhizal transport (Högberg 1997, Miller and Bowman 2002, Hobbie and Hobbie 2006), soil rooting depth (Nadelhoffer et al. 1996), and a variety of other N cycling and uptake factors (Högberg 1997). The combined use of stable N isotope analysis and N accounting within a removal experiment can therefore provide insights into the degree to which N niches overlap between neighbors, and whether plasticity exists in these niche relationships over ecologically meaningful time scales (Nadelhoffer et al. 1996, Miller and Bowman 2002, Ashton et al. 2008).

One factor that may be an important determinant of the resource–use interactions (i.e., their niche relationships) between neighbors is the amount of resources available in the local environment (Callaway et al. 2002, Wardle et al. 2008). It is recognized that plant diversity often varies strongly with resource availability (Mittelbach et al. 2001). Some diversity theories propose that higher resource availability results in more intense competitive interactions between species, which in turn influences rates of competitive exclusion, species coexistence, and species diversity (Grime 1973, Grime 1979). Other theories propose alternative coexistence mechanisms (Tilman 1982, 2007, Tilman and Pacala 1993). Additionally, the interaction of a given species with functionally different neighbors may vary strongly across environments because specific functional groups may influence ecosystem functioning more in some environments than in others (Wardle and Zackrisson 2005, Gundale et al. 2010). Understanding whether functionally similar and different neighbors exhibit negative, neutral, or positive resource–use interactions within communities, and whether these change as a function of resource availability, is central to our understanding of several widely debated relationships in ecology, such as the effect of productivity on species diversity (Mittelbach et al. 2001, Partel et al. 2010) and the reciprocal effect of species diversity on ecosystem productivity (Hooper et al. 2005).

In this study, we utilized a species and functional group removal experiment, maintained for 13 years, on a system of lake islands in the northern boreal zone in Sweden (Wardle and Zackrisson 2005, Wardle et al. 2008, Gundale et al. 2010) to determine how N acquisition, biomass, and δ^{15}N values of each of three boreal ericaceous shrub species was affected by the removal of functionally similar neighbors (the other two shrub species) and functionally different neighbors (feather mosses and tree roots). The removal experiment was set up on each of 30 lake islands that form a postfire chronosequence, which creates a strong gradient in nutrient availability and productivity, as shown in previous studies from this system (Wardle et al. 2003a, 2012, Gundale et al. 2011b). This system allowed us to investigate whether species and functional group interactions were dependent on environmental context. We

used this system to test the following hypotheses. (1) Functionally similar species act as competitors for the same N pool; therefore the removal of coexisting shrub species would result in an increase of biomass and biomass N in the remaining shrub species, whereas their realized niche would remain the same, as indicated by unchanged $\delta^{15}N$ values. (2) The removal of whole functional groups would alter how N cycles within the system, which would lead to changes in the total biomass or biomass N by all three shrub species and a change in their niche breadth, as indicated by a shift in their $\delta^{15}N$ values. (3) The effects of species or functional group removals on biomass, biomass N, and $\delta^{15}N$ would vary across the island gradient. For the species removal experiment, we predicted that competition for N would be stronger when resource availability is high, as proposed by some theories (Grime 1973, 1979) and suggested by previous work within this study system (Wardle and Zackrisson 2005, Wardle et al. 2008, Gundale et al. 2011b). For the functional group removal experiment, we predicted that removal effects on the three shrubs would be stronger on small islands because previous work from the study system has shown that both feather mosses and tree roots have a larger influence on ecosystem processes in low-fertility than in high-fertility environments (Lagerström et al. 2007, Gundale et al. 2010). Collectively, testing these hypotheses will provide insights into how N acquisition by species is influenced by their interactions with other community members, and how these interactions change as a function of resource availability.

METHODS

Study system and experimental setup

This study was conducted in a postfire chronosequence consisting of 30 forested islands in lakes Hornavan and Uddjaure (see Plate 1), in the boreal zone of northern Sweden (65°55′ N to 66°09′ N; 17°43′ E to 17°55′ E). The islands are all of the same geologic age (all being formed by the most recent glaciation), and the only major extrinsic factor that varies among them is the frequency of wildfire, with larger islands burning more frequently than smaller ones because they have a greater probability of being struck by lightning (Wardle et al. 1997, 2003a). Previous work has shown that N is the primary resource limiting productivity across the entire island gradient (Wardle et al. 1997, 2012), with the strength of this limitation increasing as islands become smaller and time since fire increases. This corresponds with slower decomposition rates, lower plant productivity, and lower plant biomass on smaller islands relative to larger islands (Wardle et al. 1997, 2003a, 2004). The mean humus depth of large, medium, and small island is 25.2, 41.4, and 65.0 cm, respectively, and C mass is 6.4, 16.2, and 27.5 kg/m^2, respectively (Wardle et al. 2012); whereas moisture content of the humus has not been found to differ between the island size classes (Bansal et al. 2012). Variation in the severity of N

limitation across the gradient leads to an eightfold difference in tree productivity and an 18-fold difference in litterfall production between the least and most productive island within the system (Wardle et al. 2003a). A more detailed description of background soil properties, nutrient availability, and productivity differences across the gradient are described in previous studies conducted in this study system (Wardle et al. 1997, 2003a, Wardle and Zackrisson 2005, Gundale et al. 2010, 2011b).

The islands were divided into three size classes with 10 islands per class: large (>1.0 ha), medium (0.1–1.0 ha), and small (<0.1 ha), with a mean time since last major fire of 585, 2180 and 3250 years, respectively (Wardle et al. 2003a). The overstory vegetation is dominated by *Betula pubescens*, *Pinus sylvestris*, and *Picea abies*, and the ground layer vegetation consists of the dwarf shrubs *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum* and the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*. Mean annual precipitation is 750 mm, of which 350 mm is deposited during the growing season (May to September), and the mean annual temperature is +0.5°C (+13°C in July and −14°C in January).

In August 1996, we established 14 experimental plots on each of the 30 islands, each representing a different removal treatment of functional groups or species (Wardle and Zackrisson 2005, Wardle et al. 2008, Gundale et al. 2010), of which 10 were used in the present study. The study was conducted as two experiments. The "species removal" experiment consisted of a full-factorial removal of *V. myrtillus*, removal of *V. vitis-idaea*, and removal of *E. hermaphroditum* (seven plots in total), which meant that each species was subjected to four shrub neighbor treatments (no neighbors, neighbor species 1 present, neighbor species 2 present, and neighbor species 1 and 2 present). These three shrub species collectively account for >98% of vascular plant biomass in the understory (Wardle et al. 2003a). The "functional group removal" experiment consisted of a full-factorial combination of tree root removal and bryophyte removal (two crossed factors, +/− tree roots, +/− feather mosses; four plots in total). Both the species and functional group experiment used the same "no removal" plot as a control. For details regarding the initial biomass proportion of the shrub species on experimental plots prior to treatments, see Wardle and Zackrisson (2005). All plots were 55 × 55 cm, but only the center of the plot was used for foliar measurements. This plot size was appropriate for assessing N acquisition by the shrubs, given that isotope-labeling studies have shown that lateral transport of nutrient through their rhizomes is minimal (Gottlicher et al. 2008). 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 (Wardle et al. 1997, 2003a). These removal plots were also located in the vicinity of 10 m radius plots previously used to characterize NPP on each island (Wardle et al. 2003a).

The experiment has been maintained annually ever since setup in 1996 (Wardle and Zackrisson 2005), making it the longest running biodiversity manipulation experiment in a non-grassland setting. Tree removals have been performed only belowground, by annual root trenching to below the tree rooting zone around the plot borders (Coomes and Grubb 2000). Dwarf shrub removal treatments have been conducted by hand-picking individual shoots of the target species, which easily separate from the humus while making only a minor disturbance. It is recognized that both root trenching and vegetation removals impose initial disturbance effects, but these are likely to be transient (Coomes and Grubb 2000, Díaz et al. 2003) and, given the long duration of the study, are likely to be of minimal importance after the first few years. Physical removal of shrubs and feather mosses each year following the initial removal is a negligible disturbance effect; the shrub species are all clonal and only slowly grow into the plots from outside them (Wardle and Zackrisson 2005).

Plant tissue analysis

In order to quantify how plant %N and $\delta^{15}N$ responded to neighbor presence or absence, we collected at least 10 leaves from mature shrubs in the center of each plot (when present) between 1 and 18 August 2009. This sampling period was at the period of maximum leaf expansion (Bansal et al. 2012) and before leaf senescence began. Collected leaves were dried in an oven at 60°C for 48 h. Leaves were then ground in a ball mill and samples were placed in tin capsules, weighed, and then folded. Stable N isotope ratios and %N were measured on samples using a mass spectrometer (DeltaPlus XP, Thermo Electron, Bremen, Germany) coupled with an elemental analyzer (Flash EA 1112, Thermo Electron). For $\delta^{15}N$, the precision of the on-line procedure was better than ±0.2‰. The natural abundance of ^{15}N was expressed in per mil (‰) deviation from atmospheric nitrogen: $\delta^{15}N = (^{15}N/^{14}N(\text{sample})/^{15}N/^{14}N(\text{atmosphere}) - 1) \times 1000$.

In order to assess the response of each shrub species (*E. hermaphroditum*, *V. myrtillus*, and *V. vitis-idaea*) to the presence or absence of their neighbors, we estimated aboveground biomass for each species in all plots where they occurred, using the point intercept method (Wardle et al. 2003a) during 1–18 August 2009. According to this method, we recorded the total number of times the vegetation of each species is intercepted by a total of 100 downwardly projected points located throughout the plot. The total number of intercepts for each species was then converted to biomass per unit area through equations previously developed by destructively sampling calibration plots (Wardle et al. 2003a). The biomass and percentage N value of each species in each plot were then multiplied to create a relative estimate of biomass N, which allowed for an evaluation of neighbor effects.

Statistical Analysis

For the species removal experiment, three separate three-factor nested ANOVAs were performed for each

shrub species (*V. myrtillus*, *V. vitis-idaea*, and *E. hermaphroditum*), with the other two neighboring species serving as fixed factors (present or absent) that were nested within island size class. For the functional removal experiment, data were first analyzed using a four-factor double-nested ANOVA, with shrub species within the plot (*V. myrtillus*, *V. vitis-idaea*, and *E. hermaphroditum*), feather mosses (removed or not removed), roots (removed or not removed), and island size (small, medium, and large) serving as fixed factors. This ANOVA model was constructed with species nested within removal treatments, and removal treatments nested within island size classes. In order to understand the response of individual species to treatments, we used post hoc three-factor ANOVAs for each species, with removal treatments (factorial combination of feather moss and tree root removal) nested within island size. In order to determine the response of whole-plot shrub biomass in response to the removal treatments, we performed separate two-factor nested ANOVAs for each experiment, with species or functional removal treatments nested within island size.

For all analyses, individual islands served as the unit of replication, with a sample size of 10 for each of the three size classes. All data were evaluated for assumptions of normality and homoscedasticity, and were transformed (by $\ln(X + 1)$) as necessary to meet these assumptions. Post hoc S-N-K (Student-Newman-Keuls) tests were performed whenever significant effects were graphically depicted. All data analyses were conducted in SPSS (version 19.0) statistical software.

RESULTS

The initial ANOVA from the functional removal experiment included a comparison of the three shrub species and showed significant differences for biomass, %N, biomass N, and $\delta^{15}N$ (Appendix A; Fig. 1a–d). *Vaccinium vitis-idaea* had the largest biomass and *E. hermaphroditum* had the least (Fig. 1a). *Vaccinium myrtillus* had the highest foliar %N content, whereas *V. vitis-idaea* had the lowest (Fig. 1b). The biomass N of both *V. myrtilus* and *V. vitis-idaea* was higher than that of *E. hermaphroditum* (Fig. 1c), and the $\delta^{15}N$ of *V. myrtillus* was significantly higher than that of the two other shrub species (Fig. 1d). Both the species and functional group removal experiments were used to evaluate the effect of island size on shrub properties. These analyses showed numerous significant effects of island size on biomass, %N, biomass N, and $\delta^{15}N$ for all three species (Appendix A; Tables 1 and 2, Fig. 1). In the species removal experiment, island size influenced all of these responses except for the %N of *V. vitis-idaea* and *E. hermaphroditum*, which remained unchanged (Table 1); in the functional removal experiment, only the %N of *V. vitis-idaea* and $\delta^{15}N$ *E. hermaphroditum* were unaffected by island size (Table 2, Fig. 1a–d). Both experiments also showed that the total biomass and biomass N of *V. myrtillus*, *V. vitis-idaea*, and *E.*

hermaphroditum reached their maximum on large, medium, and small islands, respectively (Tables 1 and 2, Fig. 1a, c). These experiments showed that foliar %N of *V. myrtillus* was significantly higher on large than on small or medium islands, whereas for *E. hermaphroditum* %N was significantly higher on small than on medium or large islands (Tables 1 and 2, Fig. 1b). No change in % N for *V. vitis-idaea* was detected across the gradient in either the species or functional removal experiment (Table 2, Fig. 1b). The species removal experiment showed that the $\delta^{15}N$ for all species significantly decreased as island size increased (Table 1); whereas the functional removal experiment showed that a significant decrease of $\delta^{15}N$ only occurred for *V. myrtillus* and *V. vitis-idaea* (Table 2, Fig. 1d).

For the species removal experiment, numerous effects of neighbor removal on total biomass and biomass N were detected for the three species, whereas $\delta^{15}N$ and %N were always unresponsive to neighbor removal (Table 1). For *V. myrtillus*, biomass N significantly increased in response to removal of *V. vitis-idaea* and *E. hermaphroditum* (Table 1, Fig. 2a, b), with corresponding increases in total biomass (Table 1; data not graphically presented). For *V. vitis-idaea*, a significant interactive effect of island size and *V. myrtillus* removal on biomass and biomass N was also detected, with the effect of *V. myrtillus* removal being stronger on large than on medium or small islands (Table 1, Fig. 2c). A significant main effect of *E. hermaphroditum* removal on *V. vitis-idea* biomass was also detected (Table 1), with the strength of this effect being greater on small islands than on medium or large islands (Fig. 2d). For *E. hemaphroditum*, both biomass and biomass N significantly increased in response to *V. vitis-idaea* removal, whereas *V. myrtillus* removal had a significant effect on biomass, but not biomass N (Table 1, Fig. 2e, f).

For the functional removal experiment, the initial four-factor ANOVA testing for effects of island size, root removal, feather moss removal, and shrub species (and their interactions), found numerous interactive effects between species and removal treatments for biomass, %N, biomass N, and $\delta^{15}N$ (Appendix A), suggesting that post hoc ANOVAs for each individual species were necessary. These post hoc ANOVAs showed significant main effects of tree root removal on $\delta^{15}N$ for both *V. myrtillus* and *E. hermaphroditum* (Table 2, Fig. 3a), with *V. myrtillus* decreasing and *E. hermaphroditum* increasing in response to removal. There was also a significant root removal × island size interaction effect on *E. hermaphroditum* biomass and biomass N (Table 2) that was caused by a significant increase in biomass and biomass N in response to root removal, but only on small islands (Fig. 3b). The data also showed a significant main effect of feather moss removal on the biomass and biomass N of *V. myrtillus* and the biomass of *V. vitis-idaea*, and an almost significant effect on the biomass N of *V. vitis-idaea* (Table 2). As such, *V. myrtillus* positively responded to feather moss removal, whereas *V. vitis-idaea* responded negatively (Fig. 4a). The
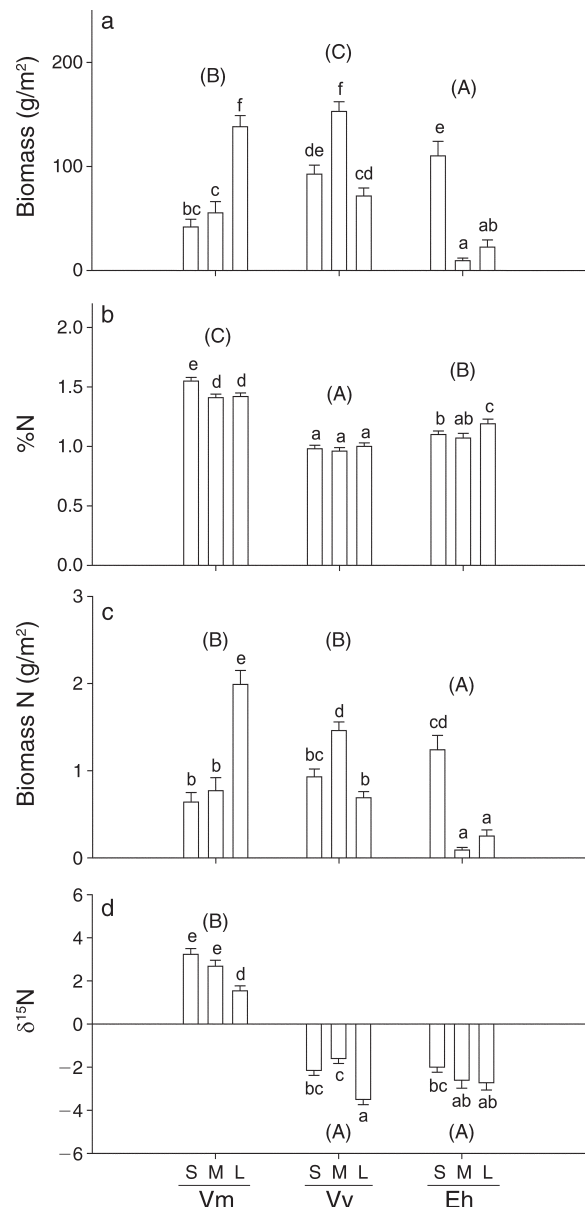

FIG. 1. Total biomass, biomass N, %N, and $\delta^{15}N$ (data shown as mean + SE) for three shrub species, *Vaccinium myrtillus* (Vm), *V. vitis-idaea* (Vv), and *Empetrum hermaphroditum* (Eh), within three island size classes (small, S; medium, M; large, L; $n = 10$ for each size) in lakes Hornavan and Uddjaure, boreal northern Sweden. Data are derived from the functional group removal experiment and were analyzed using a nested ANOVA (Appendix A: Table A1). Significant pairwise differences among the shrub species ($\alpha = 0.05$) are indicated with different uppercase letters in parentheses; significant pairwise differences between bars within each subfigure are indicated with different lowercase letters above the bars.

%N of *E. hermaphroditum* also responded to feather moss removal, as indicated by a significant main feather moss removal effect, and a significant feather moss × island size interaction (Table 2) due to a significant decline on the large, but not the medium or small, islands (Fig. 4b).

TABLE 1. Effects of species removal (Vm, Vv, Eh), island size (IS; small, medium, and large; $n = 10$ for each size), and all two- and three-way interaction effects on biomass, foliar %N, biomass N, and foliar $\delta^{15}N$ for each of three shrub species on islands in lakes Hornavan and Uddjaure, boreal northern Sweden.

Species and factor	df	Biomass		Foliar %N		Biomass N		Foliar $\delta^{15}N$	
		F	P	F	P	F	P	F	P
Vaccinium myrtillus (Vm)									
IS	2, 18	**32.18**	**0.000**	**13.06**	**0.000**	**29.11**	**0.000**	**23.65**	**0.000**
Vv	1, 9	**7.76**	**0.006**	0.01	0.915	**7.19**	**0.009**	1.91	0.188
Eh	1, 9	**6.25**	**0.014**	0.37	0.546	**5.98**	**0.016**	0.12	0.726
IS × Vv	2, 18	1.00	0.369	0.07	0.937	0.56	0.574	0.54	0.587
IS × Eh	2, 18	0.23	0.796	0.29	0.746	0.21	0.808	0.37	0.692
IS × Vv × Eh	2, 18	0.18	0.832	0.47	0.620	0.07	0.929	0.67	0.513
Vv × Eh	1, 9	0.37	0.546	0.10	0.755	0.27	0.607	0.16	0.688
Vaccinium vitis-idaea (Vv)									
IS	2, 18	**8.69**	**0.000**	1.13	0.326	**9.97**	**0.000**	**19.46**	**0.000**
Vm	1, 9	1.77	0.186	0.79	0.375	2.20	0.141	0.41	0.839
Eh	1, 9	**3.87**	**0.050**	0.02	0.894	3.23	0.075	0.09	0.766
IS × Vm	2, 18	**3.44**	**0.036**	0.25	0.780	**3.32**	**0.040**	0.13	0.876
IS × Eh	2, 18	2.89	0.060	0.48	0.621	1.96	0.146	0.34	0.713
IS × Vm × Eh	2, 18	0.11	0.900	0.30	0.743	0.09	0.918	0.03	0.970
Vm × Eh	1, 9	0.18	0.676	0.31	0.580	0.04	0.850	0.13	0.725
Empetrum hermaphroditum (Eh)									
IS	2, 18	**17.88**	**0.000**	2.10	0.130	**16.79**	**0.000**	**3.92**	**0.024**
Vm	1, 9	1.96	0.165	0.08	0.784	1.59	0.210	0.01	0.959
Vv	1, 9	**14.48**	**0.000**	0.62	0.434	**12.74**	**0.001**	0.01	0.941
IS × Vm	2, 18	0.23	0.798	0.38	0.685	0.43	0.649	0.08	0.926
IS × Vv	2, 18	1.35	0.266	0.38	0.685	0.96	0.388	0.26	0.772
IS × Vm × Vv	2, 18	0.70	0.501	0.96	0.387	0.68	0.510	0.27	0.763
Vm × Vv	1, 9	0.24	0.626	0.91	0.345	0.13	0.720	0.12	0.734

Note: Values are ANOVA statistics, with significant effects ($\alpha = 0.05$) indicated in bold.

In the species removal experiment, we found that whole-plot shrub biomass significantly differed between island size classes and between species removal treatments, and that a significant interaction between removal treatments and island size classes was present (Appendix B). In the functional removal experiment, we found no significant main or interactive effects on whole-plot shrub biomass (data not presented).

TABLE 2. Post hoc ANOVA results indicating effects of functional removal treatments (R, tree root removal; M, moss removal), and island size (IS; small, medium, and large; $n = 10$ for each size) on foliar $\delta^{15}N$ and %N for the three shrub species.

Species and factor	df	Biomass		Foliar %N		Biomass N		Foliar $\delta^{15}N$	
		F	P	F	P	F	P	F	P
Vaccinium myrtillus (Vm)									
IS	2, 18	**28.08**	**0.000**	**5.58**	**0.008**	**26.15**	**0.000**	**10.69**	**0.000**
R	1, 9	1.42	0.236	0.62	0.434	1.31	0.254	**3.97**	**0.049**
M	1, 9	**4.52**	**0.036**	0.10	0.755	**4.20**	**0.043**	0.11	0.739
IS × R	2, 18	0.39	0.678	0.21	0.811	0.299	0.742	0.61	0.544
IS × M	2, 18	0.01	0.986	0.43	0.653	0.05	0.953	0.44	0.647
R × M	1, 9	0.84	0.361	0.39	0.536	0.97	0.327	0.06	0.815
Vaccinium vitis-idaea (Vv)									
IS	2, 18	**23.88**	**0.000**	0.51	0.601	**19.05**	**0.000**	**14.36**	**0.000**
R	1, 9	0.73	0.396	1.05	0.708	0.29	0.592	0.41	0.522
M	1, 9	**4.07**	**0.046**	0.54	0.465	**3.52**	**0.050**	1.55	0.216
IS × R	2, 18	0.29	0.747	0.35	0.709	0.20	0.816	1.01	0.369
IS × M	2, 18	0.91	0.406	0.01	0.974	0.55	0.580	0.10	0.906
R × M	1, 9	0.52	0.472	0.60	0.442	0.21	0.646	0.08	0.777
Empetrum hermaphroditum (Eh)									
IS	2, 18	**35.81**	**0.000**	**3.94**	**0.025**	**33.97**	**0.000**	1.79	0.176
R	1, 9	0.22	0.639	0.02	0.894	0.15	0.695	**4.01**	**0.050**
M	1, 9	0.14	0.710	**6.77**	**0.012**	0.02	0.885	0.11	0.737
IS × R	2, 18	**3.81**	**0.025**	2.22	0.118	**3.29**	**0.041**	1.58	0.214
IS × M	2, 18	0.04	0.959	**3.80**	**0.028**	0.10	0.910	0.05	0.949
R × M	1, 9	0.13	0.719	**4.98**	**0.029**	0.12	0.728	0.34	0.855

Notes: The three-way interaction between R, M, and IS was never significant and is therefore not presented. Values are ANOVA F and P values, with significant effects ($\alpha = 0.05$) indicated in bold.
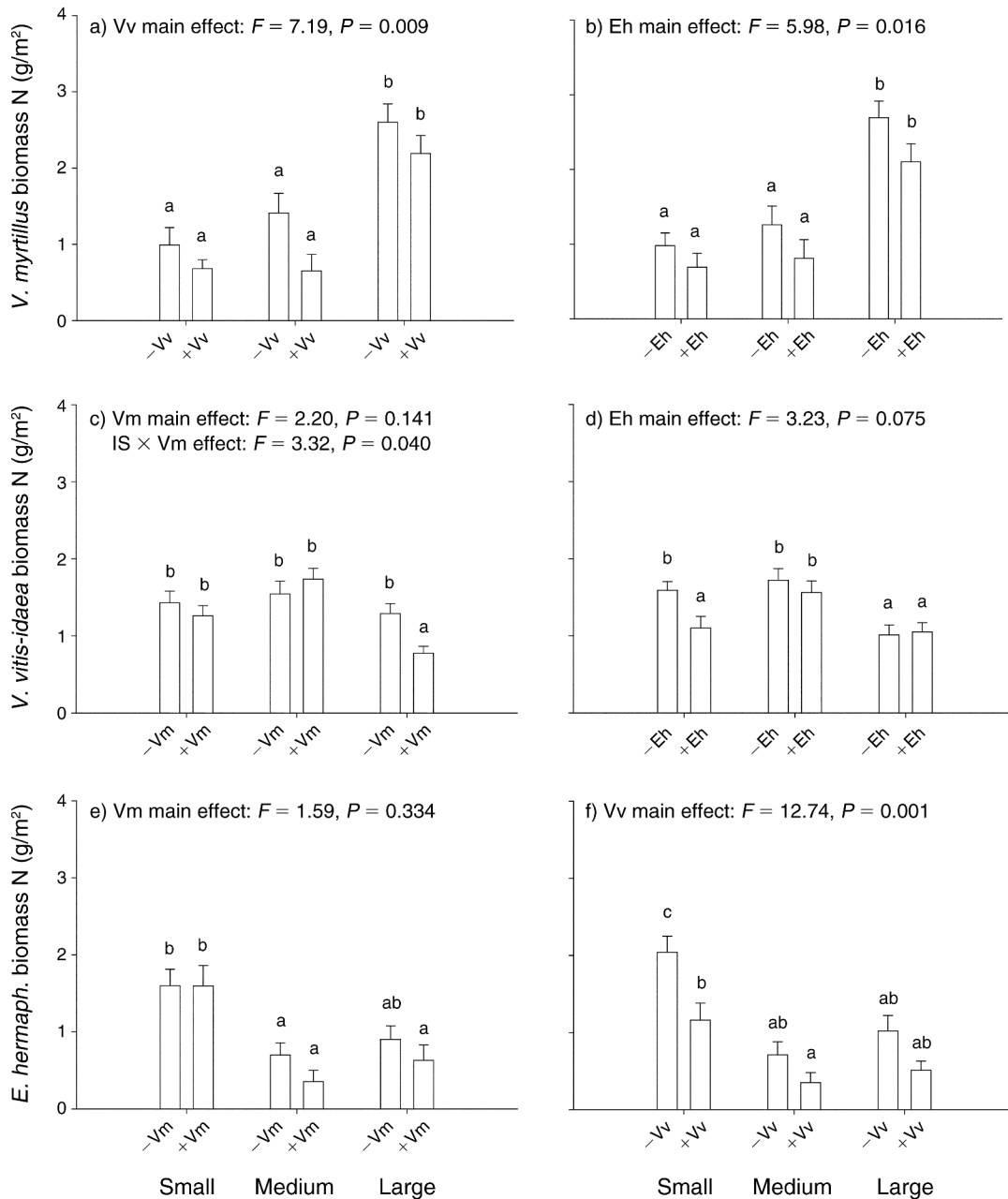
FIG. 2. Biomass N (mean + SE) of *V. myrtillus* (Vm) in response to removal of (a) *V. vitisidaea* (Vv) and (b) *E. hermaphroditum* (Eh); of *V. vitis-idaea* in response to removal of (c) *V. myrtillus* and (d) *E. hermaphroditum*; and of *E. hermaphroditum* in response to removal of (e) *V. myrtillus* and (e) *V. vitis-idaea*. Minus and plus signs indicate, respectively, that the species was removed or present. Data were analyzed using nested ANOVAs for each species (Table 1), and significant pairwise differences between bars within each subfigure (α = 0.05) are indicated with different lowercase letters. In panel (c), the island size (IS) × Vm effect was also significant (α = 0.05).

DISCUSSION

Our overarching aim was to determine whether total N acquisition and the niches of three boreal shrub species were influenced by neighbors from the same and different functional groups across a natural fertility gradient. Our data showed that, in many cases, the three shrub species significantly differed in their total biomass,

%N, biomass N, and δ^{15}N. The study system consists of a large gradient in nutrient variability and productivity (i.e., tree productivity varies eightfold and litter production by 18-fold among islands; Wardle et al. 2003a); a consequence of this, the properties of each species often varied substantially across the gradient (Fig. 1). The data also showed negative interactions between the three
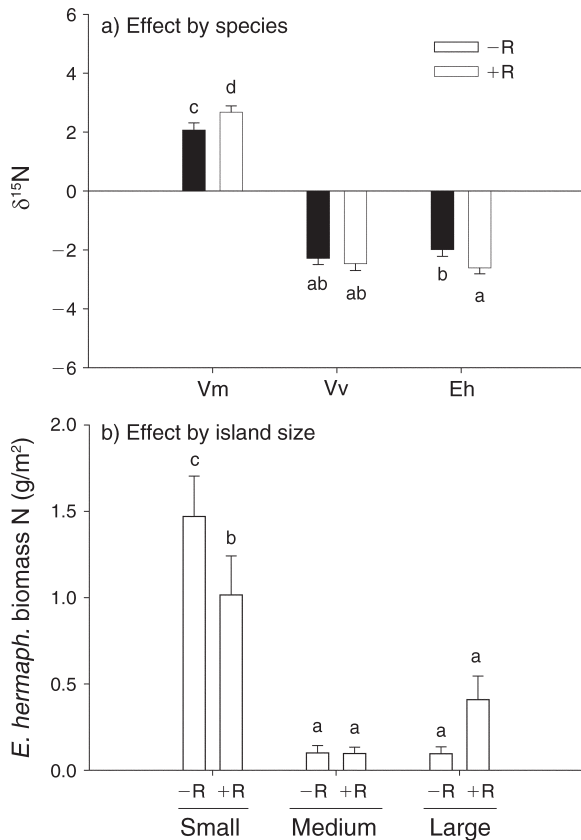
FIG. 3. Effect (mean + SE) of tree root removal (−R) on (a) foliar $\delta^{15}N$ of three shrub species (*V. myrillus*, Vm; *V. vitisidaea*, Vv; and *E. hermaphroditum*, Eh), and on (b) biomass N of *E. hermaphroditum* across islands size class (small, medium, and large; $n = 10$ for each size). Data were analyzed using a nested ANOVA for each species (Table 2). Significant pairwise differences between bars within each subfigure ($\alpha = 0.05$) are indicated with different lowercase letters.

shrub species, and both negative and positive interactions between the shrubs and the two functional groups influenced many of these properties.

Consistent with our first hypothesis, the species removal experiment showed that plant biomass N increased in response to all pairwise removal combinations for at least a portion of the island gradient (Fig. 2a–f), with the strongest effects usually involving the most abundant species within any given island size class. Also consistent with our first hypothesis, we found that plant $\delta^{15}N$ values never shifted in response to removal of neighboring shrub species, despite significant changes in total biomass and biomass N of the shrub species in response to neighbor removals (Table 1). Stable N isotope signatures of plants can be influenced by a wide range of processes (Högberg 1997), such as soil N transformations (Nadelhoffer et al. 1996), mycorrhizal transport (Högberg 1997, Hobbie and Hobbie 2006), the N species uptake, e.g., organic N vs. NH_4^+, vs. NO_3^- (Miller and Bowman 2002, Averill and Finzi 2011), and soil rooting depth (Nadelhoffer et al. 1996). The positive

increase in biomass and biomass N combined with unchanged plant $\delta^{15}N$ values resulting from the removal of neighboring shrub species suggests that these species have at least partially overlapping N niches, but that coexistence does not alter the processes, substrates, or uptake pathways utilized by each species.

In the functional group removal experiment, we found that removal of both feather mosses and tree roots had several significant effects on growth and N acquisition of the three shrub species, providing support for our second hypothesis. The removal of tree roots significantly altered the $\delta^{15}N$ values of both *V. myrtillus* and *E. hermaphroditum* (Fig. 3a). Further, the biomass and biomass N of *E. hermaphroditum* significantly increased in response to root removal on small islands, indicating competition from tree roots (Fig. 3b). Because previous work has shown that $\delta^{15}N$ of soil humus does not vary across the island gradient (Hyodo and Wardle 2009), these shifts in plant $\delta^{15}N$ values suggest that tree roots caused a change in either the uptake pathway or soil N pool exploited by these shrub species. Previous work from these plots has shown that tree root removal results
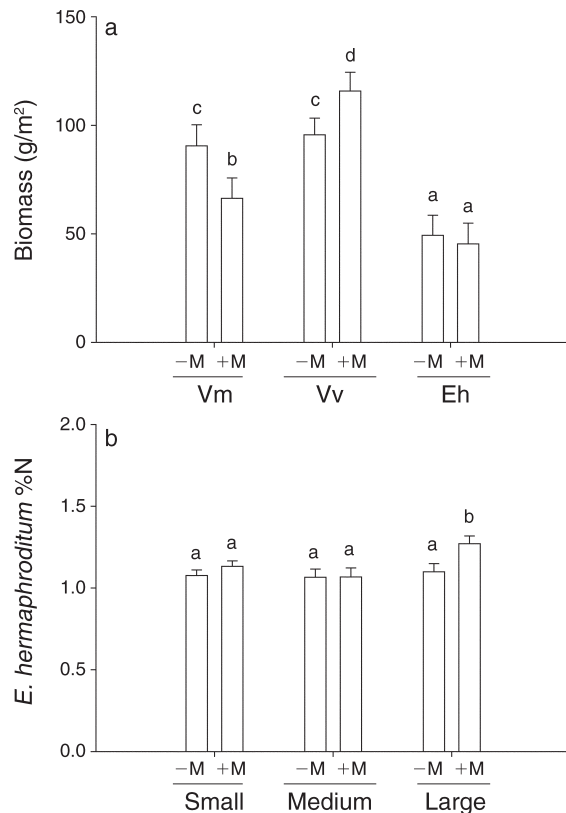

FIG. 4. Effect (mean + SE) of moss removal (−M) on (a) the biomass of three shrub species (*V. myrtillus*, Vm; *V. vitisidaea*, Vv; and *E. hermaphroditum*, Eh), and on (b) %N of *E. hermaphroditum* across island size class (small, medium, large; $n = 10$ for each size). Significant pairwise differences between bars within each subfigure ($\alpha = 0.05$) are indicated with different lowercase letters.

PLATE 1.   A series of islands formed from glacial eskers on Lake Uddjaure in Lappland, northern Sweden. Photo credit: F. Hyodo.

in a significant increase in soil inorganic N to dissolved organic N (DON) ratios (Appendix C; Wardle and Zackrisson 2005), especially on large islands where *V. myrtillus* is the most abundant shrub species. According to isotope fractionation theory, inorganic N pools are relatively more ^{15}N-depleted than organic N pools due to discrimination of the heavier N isotope during ammonification and nitrification (Evans 2007). Increased availability and utilization of inorganic N by *V. myrtillus* in response to tree root removal could therefore explain its decreased δ^{15}N. In contrast, the δ^{15}N values of *E. hermaphroditum* became less negative in response to tree root removal. This species is most abundant on the least fertile (i.e., small) islands and was most affected by tree root removals on those islands. The increase in δ^{15}N observed for this species plausibly could be driven by reduced dependence on N uptake through mycorrhizae in the absence of competing tree roots. Mycorrhizae are known to disproportionately retain ^{15}N during N transfer to their host plant, causing the host to exhibit a negative δ^{15}N value relative to the substrates taken up (Hobbie and Hobbie 2006). This could in turn explain the simultaneously higher δ^{15}N, total biomass, and biomass N of *E. hermpahroditum* resulting from tree root removal (Fig. 3). Collectively these data demonstrate that tree roots can strongly influence either the form or uptake pathway of acquired N by these two shrub species, suggesting that niche plasticity of these two species may be an important mechanism by which they coexist with trees in boreal environments (Ashton et al. 2010).

The functional removal experiment also demonstrated that all three shrub species were significantly affected by bryophyte removal. Bryophyte removal caused both the biomass and biomass N of *V. myrtillus* to increase, which indicates an antagonistic interaction; however, bryophyte removal caused biomass and biomass N of *V. vitis-idaea* and the %N of *E. hermaphroditum* to decrease, which suggests a positive interaction (Fig. 4). *Vaccinium myrtillus* is the only deciduous shrub species in the removal experiment, and therefore loses substantial N capital to the soil via litterfall each year that must be replenished through its root–mycorrhizal system (Nilsson and Wardle 2005). This deciduous strategy results in a relatively more rapid N turnover between the plant and soil, leading to higher soil inorganic N concentrations (Wardle and Zackrisson 2005). This could lead to it having a lower investment into mycorrhizae for N uptake relative to the other shrub species, and is consistent with its higher δ^{15}N value (Fig. 1d). This N-use strategy of *V. myrtillus* could also explain why it was negatively affected by feather mosses, which are known to act as strong sinks of litterfall N (DeLuca et al. 2008, Lindo and Gonzalez 2010, Gundale et al. 2011*a*). In contrast, both *E. hermaphroditum* and *V. vitis-idaea* are evergreen, have a higher N-use efficiency than *V. myrtillus*, and are therefore better able to sustain growth when turnover and availability of soil N is low (Aerts and Chapin 2000, Nilsson and Wardle 2005). Low soil N is a condition that feather mosses are likely to promote through lowering soil temperatures and producing highly recalcitrant litter (Wardle et al. 2003*b*, Lindo and Gonzalez 2010). An alternative mechanism is that the two

evergreen shrub species may be able to acquire newly fixed N directly from living feather mosses, which host N-fixing cyanobacteria (DeLuca et al. 2002, 2008), leading them to have $\delta^{15}N$ values that are more similar to atmospheric N (Hyodo and Wardle 2009). However, the $\delta^{15}N$ values of all three shrub species never changed in response to feather moss removal, suggesting that this uptake pathway is unlikely.

In support of our third hypothesis, we found that several interactions of the three shrub species with each other and with the other functional groups varied across the island gradient (Figs. 2, 3b, and 4b), which exhibits approximately an order of magnitude change in productivity. The shift in both the strength and direction of community-level interactions that we found is relevant to understanding the relationship between productivity and diversity in our study system, which is negative at the across-island scale (Wardle et al. 1997, Gundale et al. 2011b). There has been substantial debate regarding the factors that regulate diversity across gradients of productivity (Abrams 1995, Grace 1999, Craine 2005), with some theories proposing that competition is important at all levels of resource availability (Tilman 1982, 1985), and others proposing that it is more intense when productivity is higher, leading to higher rates of competitive exclusion and lower species diversity (Grime 1973, 1979). Our data are partially consistent with both of these perspectives in that the species with the most resource-demanding strategy, *V. myrtillus*, exerted its strongest negative effects in the most fertile and productive environments (i.e., large islands; Fig. 2c). However, the data also clearly show that competition, as well as neutral and positive interactions, were present at all levels of productivity, suggesting that species diversity is probably influenced by the net combination of community-level interactions at any given level of productivity (Mittelbach et al. 2001, Zobel and Partel 2008). Our data are also highly relevant for understanding the reciprocal effect that diversity may have on productivity in our study system, which has been the source of substantial debate during the past two decades (Hooper et al. 2005). It is proposed that positive biodiversity–function relationships may occur as a result of either resource–use complementarity among coexisting plant species or positive species interactions (Hooper et al. 2005). Our data show that the relationships of any given species with its neighbors (i.e., negative, neutral, and positive) differ substantially for different combinations of neighbors; and further, that for any given pair of neighbors, the strength or direction of these interactions frequently varies strongly with productivity (i.e., across island size classes). These data help to explain our previous results from this study system showing that the effect of diversity loss on ecosystem functioning is strongly dependent on both the identity of the species lost and the environmental context from which the loss occurs (Appendix B) (Wardle and Zackrisson 2005, Wardle et al. 2012), rather than biodiversity loss per se.

CONCLUSIONS

Our use of N accounting and stable N isotope analysis within the context of a long-term neighbor removal experiment (13 years) provides a novel method to assess plant N niche interactions. Previous studies using ^{15}N-labeled soluble N substrates as a tool to assess plant N niches have reached contradictory conclusions, with some providing strong support for N-use complementarity (e.g., McKane et al. 2002, Ashton et al. 2010) and others providing limited evidence (e.g., Nordin et al. 2004, Harrison et al. 2007). Our study provides a complementary long-term approach to isotope-labeling studies, and yields several new insights into understanding plant N niches. First, our data suggest that N-use interactions between functionally similar neighbors (i.e., the three ericaceous shrubs) are usually negative, suggesting that their N niches at least partially overlap, and that coexistence between the shrub species within local communities occurs despite some degree of competition for N. Secondly, our data show that two functional groups, trees and feather mosses, each have strong effects on the N acquisition of the three shrubs. However, whether these effects are positive, competitive, or complementary depends on which species and functional groups are considered, suggesting that a fundamental difference in the N niches of the three shrub species involves their interaction with these functional groups. We have also showed that, in some cases, the removal of a functional group, notably tree roots, results in an alteration of shrub $\delta^{15}N$ values, which suggests that plasticity in either N substrate utilization or transport may serve as a coexistence mechanism between shrubs and trees in this system. Finally, the improved understanding of community-level interactions revealed through this study provides insights into the reciprocal relationship between species diversity and productivity, and suggest that the individualistic niche characteristics of community members across environmental gradients are likely to play an important role in determining whether and how productivity and diversity are linked to one another.

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SUPPLEMENTAL MATERIAL

Appendix A

An analysis of variance (ANOVA) table showing the *F* and *P* values of a functional-group removal experiment (*Ecological Archives* E093-147-A1).

Appendix B

A figure showing the effect of species removal treatments on total plot biomass measured in August 2009 (*Ecological Archives* E093-147-A2).

Appendix C

A figure showing the effect of tree root removal on dissolved inorganic nitrogen to dissolved organic nitrogen ratios in small, medium, and large island size classes (*Ecological Archives* E093-147-A3).