



Resource heterogeneity does not explain the diversity–productivity relationship across a boreal island fertility gradient

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Many studies at the regional scale have found either negative or hump-shaped relationships between productivity and diversity, and some theories propose that these occur because soil resource heterogeneity is either lower or less important in more productive environments. However, there have been few explicit tests of these theories in natural ecosystems. We evaluated the relationship between soil resource heterogeneity and plant richness within a well characterized system of 30 islands in northern Sweden across which soil fertility and productivity declines, and species richness increases, as a consequence of ecosystem retrogression. On each island we created a spatially explicit grid consisting of 49 sampling points in a 9.5 m quadrat, which we used to quantify spatial heterogeneity of five soil variables (NH_4^+ -N, amino N, PO_4^- -P, microbial biomass, and decomposition), and plant community composition. Using a hierarchical Bayesian approach, we estimated mean semivariograms of each variable for each island size class to compare three components of spatial heterogeneity: total variability, spatial grain, and patchiness. This analysis showed that variability within islands was usually lowest on small islands, where species richness was highest and productivity lowest; however, NH_4^+ -N and amino N had greater patchiness and spatial grain on small islands. We did not detect any significant across-island correlations between whole-plot plant species richness and either whole-plot standard deviation or coefficient of variation of any soil variable. Using partial Mantel tests, we found that mean correlation coefficients between within-plot plant community composition and the soil variables were never significant for any island size class, and did not differ between island size classes. Our findings do not provide any evidence that soil resource heterogeneity controls the productivity–diversity relationship in this system, and suggests other mechanisms are primarily responsible.

A central focus in ecology is to understand the underlying mechanisms that generate and maintain patterns of species diversity. One factor that is often considered to be of importance in determining plant species diversity is the heterogeneity of limiting resources (Hutchinson 1959, Tilman 1982, Tilman and Pacala 1993, Huston and DeAngelis 1994). The resource heterogeneity hypothesis (RHH) proposes that for a given area, increasing resource heterogeneity increases the number of species that can coexist, resulting in higher species diversity (Hutchinson 1959, Ricklefs 1977, Tilman 1982, Tilman and Pacala 1993, Mittelbach et al. 2001). This is proposed to occur because plant community members have different resource niches that allow each species to be competitively dominant under a different combination of local resource conditions (MacArthur and Levins 1967, Ricklefs 1977, Reynolds et al. 2007). Therefore, according to the RHH, areas with variable resource conditions will result in patch-scale

dominance of different species, and will therefore result in higher diversity relative to areas with spatially homogeneous resource conditions (Tilman and Pacala 1993).

The general premise of the RHH has been incorporated into several theories that aim to explain the relationships between productivity and diversity (Tilman and Pacala 1993, Huston and DeAngelis 1994, Abrams 1995). Productivity–diversity relationships are often observed to be negative or hump-shaped (Ricklefs 1977, Tilman and Pacala 1993, Grace 1999, Mittelbach et al. 2001), and the underlying mechanisms that control this pattern have been the subject of substantial debate (Abrams 1995, Waide et al. 1999, Craine 2005). Several models have proposed that decreasing diversity at high levels of productivity occurs because of a decrease in soil resource heterogeneity as productivity increases (Tilman 1982, Tilman 1987, Abrams 1988). Other diversity models have suggested that diversity decreases at high levels of productivity because there is a

shift in limitation from soil resources, which are inherently heterogeneous because they are supplied in three-dimensional space, to limitation by light, which is inherently homogeneous because it is supplied vertically (Tilman and Pacala 1993, Huston and DeAngelis 1994, Abrams 1995). Huston and DeAngelis (1994) further proposed that plant species themselves generate greater heterogeneity of limiting soil resources in low productivity environments (but not high productivity environments) because nutrient depletion zones develop around plants only when soil resources are limiting, such as is the case in unproductive environments. This increase of heterogeneity associated with nutrient depletion zones in unproductive environments is proposed to create more variable niche conditions that result in a greater number of co-existing plant species.

These theories predict that either lower heterogeneity of soil resources should occur in high productivity environments or that spatial variation in plant community composition should be less coupled to variation in soil resources in high productivity than in low productivity environments. Conversely, Abrams (1995) argued that there is no inherent reason why resource heterogeneity should be lower in high productivity settings, and various other mechanisms have been proposed to explain the negative or hump-shaped productivity–diversity relationships (Grime 1979, Abrams 1995). Despite the implied importance of resource heterogeneity in some productivity–diversity theories, and much debate regarding the underlying mechanisms that generate productivity–diversity patterns (Abrams 1995, Waide et al. 1999, Lavers and Field 2006), surprisingly few studies have explicitly quantified soil resource heterogeneity across gradients of plant productivity and diversity (Gross et al. 1995, Lundholm and Larson 2003, Bartels and Chen 2010).

In this study we use a well-described gradient of plant productivity and diversity in northern Sweden (Wardle et al. 1997, 2003) to explicitly test whether there is an underlying relationship between soil heterogeneity, plant species diversity and plant productivity, as predicted or assumed by several productivity–diversity models (Tilman 1982, Tilman and Pacala 1993, Huston and DeAngelis 1994). This gradient consists of 30 forested islands, in which island area determines the frequency of lightning ignited wildfire and therefore historical fire regime. Previous studies on these islands have shown that as time since fire increases the islands undergo ecosystem retrogression (Wardle et al. 2004), with a marked decline in nutrient availability and therefore ecosystem productivity, and a corresponding increase in plant species richness per unit area (Wardle et al. 2008a). This system lends itself to testing whether an underlying positive relationship exists between diversity and resource heterogeneity at the regional scale (i.e. across islands) that may explain the observed negative relationship between diversity and productivity. Because species diversity is highest, and productivity is lowest, on small islands, we first hypothesized that spatial heterogeneity of soil characteristics per unit area would be greatest on small islands. Specifically, we predicted that with decreasing island size, soil characteristics would become more heterogeneous, meaning they would be more spatially variable, and exhibit a coarser and more strongly defined patch structure. Secondly, we hypothesized that across all islands,

there would be a positive relationship between variability of soil parameters and species richness, with islands showing the greatest variability of soil characteristics also having the highest number of species per unit area. Thirdly, we hypothesized that at the within-island scale, spatial variation in plant community composition would be correlated with spatial variation in key soil parameters, (consistent with the RHH) (Ricklefs 1977, Tilman and Pacala 1993); and further, that the strength of these correlations would increase as productivity decreases. This pattern would be consistent with theories that propose the reduced importance of soil resource heterogeneity as a driver of plant diversity in high productivity settings (Tilman 1982, 1987, Huston and DeAngelis 1994). Collectively, these three hypotheses explicitly test the RHH, and further address whether the ‘regional’ (across-island) negative relationship between plant diversity and productivity in this study system is controlled by an underlying influence of soil resource heterogeneity on diversity.

Methods

Study system and vegetation measurements

We performed this study during August 2008 and August 2009 on a fertility gradient occurring across 30 forested islands in lakes Hornavan and Uddjaure in the boreal zone of northern Sweden ($65^{\circ}55'N$ – $66^{\circ}09'N$, $17^{\circ}43'E$ – $17^{\circ}55'E$). The mean annual precipitation is 750 mm, and the mean temperature is $+13^{\circ}C$ in July and $-14^{\circ}C$ in January. All islands were formed from unconsolidated granite boulders deposited by glacial eskers that formed following the retreat of land ice about 9000 yr ago. The only major extrinsic factor that varies among islands is the history of lightning ignited wildfire, with larger islands having burned more frequently than smaller islands because of their larger area to intercept lightning (Wardle et al. 1997, 2003). As a result, the islands form a post-fire chronosequence, with increasing time since fire as island size decreases. Previous studies on the island study system have shown that as islands become smaller and time since fire increases, that islands undergo ‘ecosystem retrogression’ (Peltzer et al. 2010), meaning there is a reduction in nutrient availability, decomposition rates, microbial biomass, light interception, plant productivity and plant biomass, and an increase in humus depth and plant species diversity (Wardle et al. 1997, 2003, 2004). We note that the negative relationship between island area and species richness present in this study system is inconsistent with predictions of most neutral diversity models, such as the theory of island biogeography (MacArthur and Wilson 1967), which makes it possible to use this study system to investigate other mechanisms that may control diversity without confounding effects of island area. Further, dispersal limitation does not affect access of plant species to islands, and all plant species present in the system are present on even the smallest and most isolated islands.

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 yr, respectively (Wardle et al. 2003).

No fires have occurred on any of the island within at least 60 yr (and up to 5350 yr ago), which is sufficient time for understory communities to re-establish; shrub and moss biomass on the large most recently burned islands is at least as large as for the smaller islands (Wardle and Zackrisson 2005, Wardle et al. 2008b). Further, the more frequent fires that occur on the large islands are not stand replacing, and mean stand age is actually greatest on the most recently burned islands though does not significantly differ between island size classes (mean age of the oldest tree in 10 m radius plots (\pm SE) for small, medium, and large islands is 232 (\pm 35), 306 (\pm 23), and 357 (\pm 47), respectively). The overstory vegetation of the island system is dominated by *Pinus sylvestris*, *Betula pubescens*, and *Picea abies*, which have their greatest biomass on large, medium and small islands respectively. The ground layer vegetation is dominated by the feather mosses *Pleurozium schreberi* and *Hylocomium splendens*, which decrease slightly in biomass with increasing island size, and the dwarf shrubs *Vaccinium myrtillus*, *V. vitis-idaea*, and *Empetrum hermaphroditum*, which have their greatest biomass on large, medium and small islands respectively (Wardle et al. 2003).

Within each island, we established a 9.5×9.5 m plot (hereafter referred to as a 'whole-plot') directly adjacent to a set of pre-existing experimental plots used for previous studies on the island (Wardle et al. 2003, Wardle and Zackrisson 2005). All whole-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, 2003). Within each whole-plot, 49 sampling points were established in a semi-randomized grid pattern, configured to ensure that sample points occurred at varying distances from one another to maximise the power of spatial statistical analysis (Fortin and Dale 2005). This sampling design resulted in 1470 sample points for each response variable measured (i.e. 49 points \times 30 islands).

On each island, understory plant species richness at the whole-plot level was estimated by sampling at each of the 49 sampling points (hereafter referred to as sub-plots). Each subplot consisted of a 5 cm diameter circle (19.6 cm^2) in which we visually recorded the percent cover of all plant species present. A total of 26 plant species (13 vascular plants and 13 bryophytes) were found across the entire study system. These data were used to provide an estimate of species richness for each island whole-plot. Further, an ordination was performed on all sub-plot data from all islands (1470 subplots in total) using principle component analysis (PCA), in order to reduce the plant community composition data at the subplot level to a smaller number of variables (PCA; Primer 6, Luton, UK). Prior to analysis, cover values for all species within each sub-plot were converted to proportions of total cover within that subplot. The first and second ordination axis scores were both used as relative measures of plant species composition.

Soil sampling and measurements

In order to quantify soil heterogeneity, we focused on two-dimensional heterogeneity of the surface 10 cm of the humus layer because all understory vascular plants in this

system root entirely within this depth, and because two-dimensional spatial heterogeneity rather than vertical heterogeneity is more likely to explain plant spatial patterns and thus the increase in species diversity found on small islands. At each sampling point used to measure plant species data on each island (i.e. subplots), we measured 5 variables that are indicative of soil resource availability. Three of these involve available forms of nutrients previously shown to be limiting in the system (Wardle et al. 1997, 2004), i.e. extractable NH_4^+ -N, amino N, and PO_4^- -P. The other two were substrate induced respiration (SIR) which is a relative measure of the active microbial biomass responsible for regulating the supply of plant-available nutrients from the soil, and the rate of decomposition of a standardized substrate which is indicative of the ability of the soil biota to break down organic substrates and thus release nutrients. Soil sampling was conducted by collecting humus cores (0–10 cm depth) at each sampling point within each island, using a 50 mm diameter sampling auger with a serrated edge. Upon collection, each soil sample was placed in a polyethylene bag, placed in a cooler and transported to a nearby refrigeration facility, and stored at 2°C until sampling of all islands was complete. At the end of sampling, all samples were sieved (4 mm) and extracted in the same order as they were collected, so that the time between sampling and extraction was equal for all samples. For each sample, 5 g sieved soil (wet weight) was extracted with 1 M KCl, and colorimetrically analyzed for NH_4^+ -N, amino N, and PO_4^- -P on an Auto-Analyzer III (Omni Process, Solna, SE). In addition, ca 5 g of each sample was used for determination of gravimetric water content, which allowed nutrient concentration measures on all extracts to be determined on a soil dry weight (d.w.) basis. Measurements of relative active soil microbial biomass (SIR method; Anderson and Domsch 1978) were made on a 5 g subsample of soil (d.w.) for each soil sample. Each subsample was placed into a 100 ml glass bottle, and the volume of water needed to raise the soil moisture content to 225% (d.w. basis) was added. After water addition, samples were placed in a dark incubator (15°C) overnight to equilibrate. The following day, 2.5 ml of glucose solution (40 g l^{-1}) was pipetted into each bottle, which increased the water content of the soil to ca 250%, and added a quantity of glucose equivalent to 2% soil dry weight. The jar was then sealed, and evolution of CO_2 between 1 and 4 h following glucose addition was then determined by injecting 1 ml subsamples of headspace gas into an infrared gas analyser, which allowed for estimation of SIR.

The decomposability of plant litter was measured at each sampling point on each island by using litter bags with mesh size 0.1 mm, with each containing a uniform substrate, i.e. 1 g of dried *P. sylvestris* needle litter. For each subplot, one litter bag was placed vertically at a depth spanning 0–2 cm from the surface of the humus during August 2008, and harvested one year later during August 2009. After harvest, the remaining litter was removed from each bag, dried for 48 h (65°C), and weighed. Data were calculated as percentage loss of the initial mass.

Statistical analysis

We tested for mean differences in the five soil variables (i.e. NH_4^+ -N, amino N, PO_4^- -P, SIR, and decomposition) and species richness between island size classes using a one-way analysis of variance (ANOVA) for each variable, with island size class (small, medium, and large) serving as a fixed factor ($n = 10$), and with individual islands serving as the units of replication. As such, for the soil variables, each data point was calculated as the mean of all 49 sample points within the whole-plot. Species richness per unit area for each island was calculated as the cumulative number of species found across the 49 sample points on each island. All comparisons used an alpha of 0.05 ($DF = 2,29$), and were followed by S-N-K pairwise post-hoc tests when significant differences were detected.

We tested our first hypothesis, that spatial heterogeneity for each variable (i.e. NH_4^+ -N, amino N, PO_4^- -N, SIR, decomposition, PCA1 and PCA2) would differ between island size classes, by computing empirical semivariograms for each variable, which were then used to estimate mean spatial heterogeneity parameters for each size class. A semivariogram is composed of semivariances, which are estimates of variability for points separated by a defined distance. In an empirical semivariogram, the estimated semivariances are plotted on the y-axis against lag distance (h) on the x-axis. The empirical semivariogram is used to estimate secondary parameters that describe several components of spatial heterogeneity of the variable of interest, including the nugget variance (C_0), the structural variance (C), the sill ($C_0 + C$), the range, and the ratio of structural variance (C) to total variance (sill, $C_0 + C$), hereafter referred to as the proportional structural variance (PSV) (Fig. 1) (Fortin and Dale 2005). Briefly, the sill is the semivariogram asymptote and is an estimate of the total variance within sampling space. The sill is composed of two

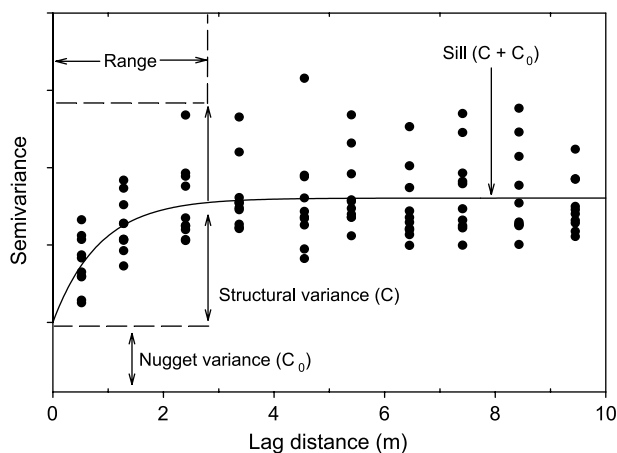


Figure 1. A representative mean semivariogram, characteristic of those created for each of the measured variables within each island size class. The empirical semivariogram data is derived from 10 islands within each size class. Using a hierarchical Bayesian approach, a best-fitting semivariogram model was used to estimate the mean ($\pm 95\%$ credible intervals) for three secondary parameters derived from the model. These parameters include the sill ($C_0 + C$), the range, and the proportion structural variance (PSV) ($C/(C_0 + C)$), where C_0 is the nugget variance and C is the structural variance.

types of variance, the structural variance and nugget variance. The structural variance is variability that is spatially aggregated within sampling space. The nugget variance consists of variance not accounted for in the empirical semivariogram, and consists of randomly distributed variation through sampling space plus measurement error. The PSV reflects the degree to which the total variance within the sampling space is spatially structured (or randomly dispersed), and thus describes the patchiness of a given variable (Fortin and Dale 2005). The range is the distance at which the semivariogram asymptote is reached, and describes the spatial scale of patchiness (i.e. spatial grain). We computed semivariograms using 10 distance classes, separated by 1 m uniform distance intervals, using GS+ software (Gammadesign Software, Plainwell, MI, USA). All semivariograms were visually evaluated for anisotropy (i.e. the occurrence of unidirectional gradients) by computing semivariograms in four opposing directions (i.e. 90° rotation), which was not found to be present in the dataset.

Spatial heterogeneity between island size classes was compared within a hierarchical Bayesian (HB) framework (Clark 2005). The HB model has three primary components: 1) the data model that describes the likelihood of the observed semivariance data (γ); 2) the process model that describes the mean or predicted γ and includes process uncertainty associated with random island effects; and 3) the parameter model that specifies prior distributions for process model parameters and variance terms. The sill, range, and PSV for each variable within each island size class were treated as unknown parameters and estimated from posterior distributions generated by combining the data model, the process model, and the parameter models (Clark 2005). This approach is useful because it allows us to explicitly account for multiple sources of uncertainty (i.e. among islands, within plots, measurement and model error), and enables an estimation of the variability associated with each of these estimates. We assumed semivariances observed from the ten replicate islands, within each island size class, at each lag distance (h), were normally distributed about a mean μ_i with precision τ (Fig. 1), a measure of observation error variability. In specifying the process model, we used four model forms commonly used in spatial statistics (i.e. linear, exponential, spherical, or Gaussian) (Fortin and Dale 2005). We also allowed for the possibility of different island behavior at each lag distance and included a random island effect to capture process error. We assigned non-informative, uniform priors to all unknown parameters and used folded-Cauchy densities (i.e. a Student's t-distribution with one degree of freedom) as priors for all standard deviations ($\sigma = 1/\sqrt{\tau}$, where τ is the precision parameter of interest) (Gelman 2006). We report posterior parameter means and 95% credible intervals for the range, sill and PSV from the model with the lowest residual sums of squares. Parameter estimates whose 95% credible intervals do not overlap are interpreted as being significantly different from each other (Clark 2005). All analyses were conducted in WinBugs ver. 3.0.2.

We tested our second hypothesis, that islands with high whole-plot variability of soil parameters would correspond with higher species richness, by calculating Pearson's correlation coefficients ($n = 30$) between whole-plot plant

species richness and two measures of whole-plot variation for each soil variable, the whole plot standard deviations (SD) and coefficients of variation (CV) (measures of absolute and relative variability, respectively). We used partial Mantel tests (Mantel 1967) to assess our third hypothesis; that within island variation in soil parameters would be correlated to variation in species composition. Within each island, the partial Mantel test enables calculation of correlations between two dissimilarity matrices (i.e. between each soil variables and plant community composition) while controlling for the effects of spatial autocorrelation by using a co-variate distance matrix (Fortin and Gurevitch 2001). Dissimilarity matrices of plant community composition were created from species relative abundance data using the Bray–Curtis dissimilarity (Fortin and Gurevitch 2001), while soil variable dissimilarity and geographic distance matrices were calculated from within-plot distance measurements (between sampling points) using Euclidean distances. In addition to using Bray–Curtis dissimilarity to describe the plant community, we also performed this analysis using the first and second axes of the PCA, which allowed us to see how different components of the plant community responded to variation in soil properties. Partial Mantel tests were computed with the R statistical platform, using the package *Vegan*. In order to compare whether differences in the strength of correlation between soil and plant community variables existed between island size classes, we tested for differences in mean partial Mantel coefficients using one-way ANOVAs for each soil variable by plant community variable combination, with island size serving as a fixed factor, and with individual islands serving as the units of replication (i.e. $n = 10$ for each size class). All data met assumption of normality and homoscedasticity and therefore did not require transformation. We additionally report the mean p value that corresponds with each mean partial Mantel coefficient in order to assess whether the mean Mantel coefficient for each variable within each island size class occurred below an alpha of 0.05.

Results

At the whole-plot scale, the total number of plant species present ranged from 4 to 14 across the 30 islands, with a total of 24, 17, and 12 species occurring within the small, medium, and large island size classes, respectively. This corresponded with significantly higher mean species richness per area on small islands at the whole plot scale (Fig. 2a). The PCA performed on all subplots produced an ordination for which 39.6 percent of the variation in species composition was explained by the first axis and 24.6 percent was explained by the second axis. The species loading scores for each axis showed that the first axis primarily represented variation in dominance by *V. myrtilus* and *V. vitis-idaea*, with loading scores of -0.617 and 0.78 , respectively. The second PCA axis primarily reflected variation in dominance by both *V. myrtilus* and *V. vitis-idaea* (loading scores -0.557 and -0.410 , respectively) and in dominance by *E. hermaphroditum*, *Linnaea borealis*, *P. schreberi*, *H. splendens*, and *Dicranum* sp. (loading scores 0.096 , 0.009 , 0.102 , 0.708 , 0.011 , respectively). Mean differences in

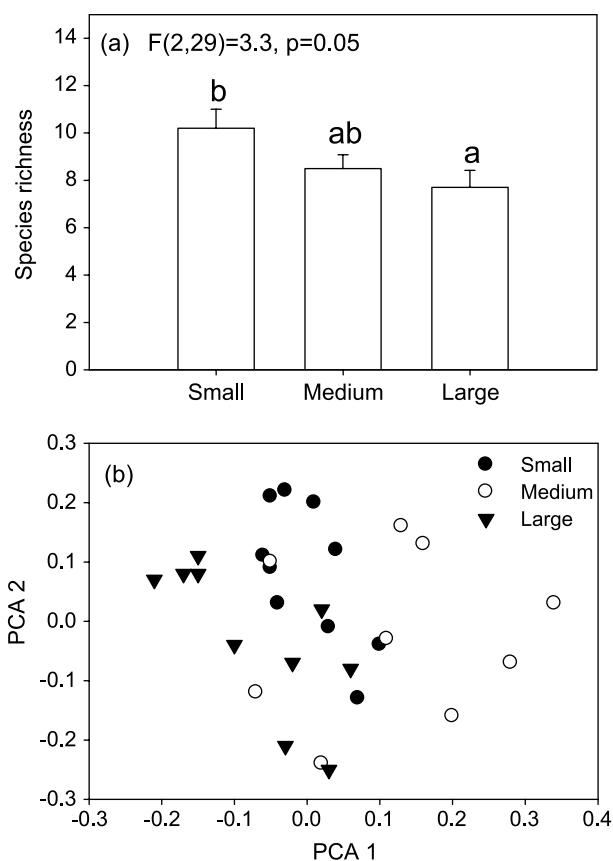


Figure 2. The mean (\pm SE) values for species richness (a), and the mean principle component analysis (PCA) position of 30 islands for the first and second PCA axis (b). Island are divided into three size classes (S = small, M = medium, and L = large), where productivity increases with island size. For the first panel, different letters above bars indicate significant differences according to an S-N-K post hoc test.

ordination axis scores between island size classes were marginally statistically significant (axis 1: $F = 2.466$, $p = 0.10$; axis 2: $F = 2.67$, $p = 0.09$; Fig. 2b).

Consistent with previously observed differences in productivity between the island classes (Wardle et al. 2003), mean differences in several soil properties between island size classes at the whole-plot level were also detected. Extractable phosphate (PO_4^- -P) concentrations and SIR values were significantly lower on small than on medium or large islands (Fig. 3a, b). Further, decomposition rates were significantly lower on small than on large islands (Fig. 4c). Both NH_4^+ -N and amino N were not significantly different between island size classes ($F = 0.706$, $p = 0.502$, and $F = 0.592$, $p = 0.560$, respectively).

Significant differences were detected between island size classes in the overall sample variance (i.e. sill), range, and patchiness (i.e. PSV) for several variables (Fig. 4a–u). Of the soil variables, the sill was significantly smaller on small islands than on medium or large islands for NH_4^+ -N, amino N, PO_4^- -P and SIR (Fig. 4a–d), whereas for decomposition the sill for both small and medium islands was significantly lower than for the large islands (Fig. 4e). Amino N and SIR had significantly higher sills for medium sized islands than for the other two size classes (Fig. 4b, d).

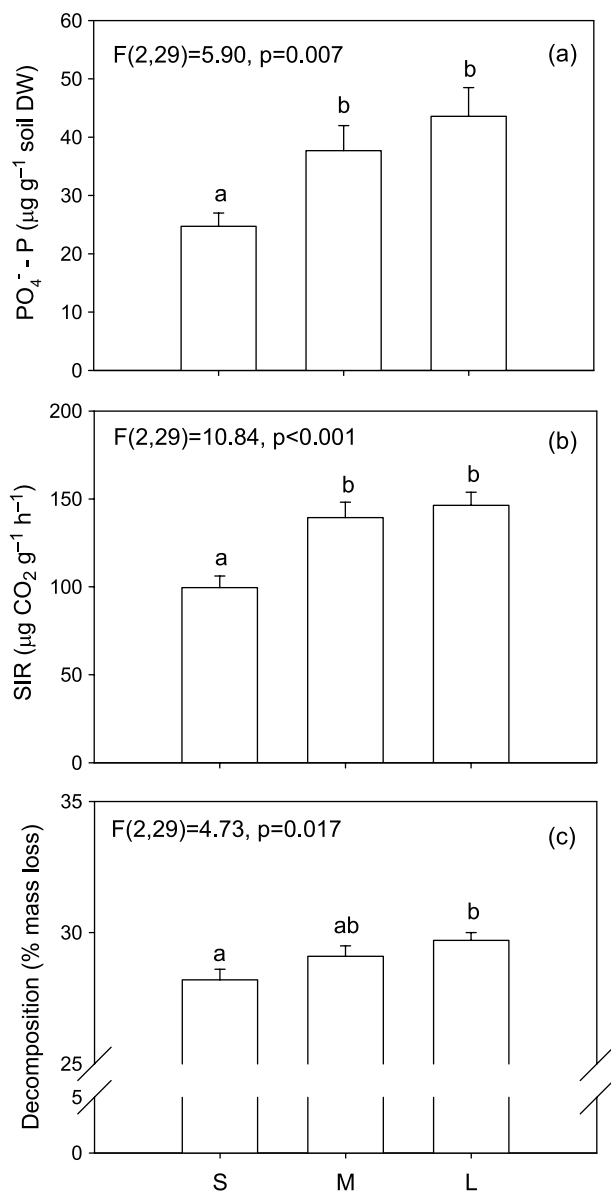


Figure 3. The mean (\pm SE) PO₄⁻-P (a), substrate induced respiration (SIR) (b), and decomposition rate (c) for three island size classes (S = small, M = medium, and L = large). Within each panel, numbers with different letters are not significantly different according to S-N-K post hoc comparisons.

For the two variables representing plant community composition, the sill for the first PCA axis scores was significantly lower for small than for large islands (Fig. 4f), whereas the sill for the second PCA axis scores showed the opposite pattern, with small islands having a larger sill than for the medium and large islands (Fig. 4g). The range also demonstrated significant differences between island classes for some variables (Fig. 4h–n). For NH₄⁺-N, the range was significantly larger for small islands than for medium and large islands (Fig. 4h). For amino N, both small and medium islands had a significantly larger range than did large islands (Fig. 4i). For phosphate, the range was significantly higher for medium islands than for small or large islands (Fig. 4j). Ranges for all other soil and plant community variables did not differ significantly between

island size classes (Fig. 4k–n). The PSV also showed some significant differences between island size classes (Fig. 4o–u). Both NH₄⁺-N and amino N had higher PSV on small islands than on medium or large islands (Fig. 4o, p), and for amino N, medium islands also had a larger PSV than did large islands (Fig. 4p). The PSV of PO₄⁻-P was higher for medium islands than for small or large islands (Fig. 4q), whereas SIR showed significantly lower PSV on small islands than on large islands (Fig. 4r). The mean PSV did not differ significantly across island size classes for decomposition or for PCA axis score values (Fig. 4s–u).

The Pearson's correlation coefficients used to evaluate the relationship between whole plot species richness and whole plot SD for each soil variable did not reveal any significant relationships across the thirty islands (n = 30) for any of the soil variables (for NH₄⁺-N: $r = -0.300$, $p = 0.107$; amino N: $r = -0.193$, $p = 0.306$; PO₄⁻-P: $r = -0.290$, $p = 0.120$; SIR: $r = 0.145$, $p = 0.446$; decomposition: $r = 0.279$, $p = 0.136$). Likewise, the relationship between whole plot species richness and the whole plot CV for each soil variable did not reveal any significant relationships across the thirty islands (n = 30) for any of the soil variables (NH₄⁺: $r = -0.052$, $p = 0.785$; amino N: $r = -0.290$, $p = 0.120$; PO₄⁻: $r = 0.121$, $p = 0.524$; SIR: $r = 0.252$, $p = 0.179$; decomposition: $r = 0.315$, $p = 0.090$).

The partial Mantel tests, which were used to evaluate correlations within each island between soil variables and plant community composition, showed that a low proportion of islands had significant correlations. For NH₄⁺-N, amino N, PO₄⁻-P, decomposition, and SIR, and a multivariate matrix composed of all of these soil variables showed significant correlations with plant species composition (using Bray–Curtis dissimilarity) for only 3, 3, 3, 3, 4 and 2 out of the 30 islands. The same analysis using PCA axis 1 and 2 to describe the plant community showed that significant within-plot correlations with soil variables (NH₄⁺-N, amino N, PO₄⁻-P, decomposition, and SIR) occurred for 3, 2, 2, 2, and 3 out of 30 islands for PCA axis 1, and 4, 3, 5, 3, and 0 islands out of 30 for PCA axis 2. A comparison of the mean partial Mantel coefficients across island size classes revealed no significant differences in mean partial Mantel coefficient between island size classes both when Bray–Curtis dissimilarity (Table 1) and PCA analysis (data not presented) was used to describe the plant community.

Discussion

Our study confirmed the previously described negative relationship between productivity and diversity observed within this island study system (Fig. 3, 4; Wardle et al. 1997, 2008a), and aimed to explicitly evaluate whether this relationship was driven by an underlying influence of soil resource heterogeneity on diversity. Specifically, we predicted that soil resource heterogeneity would increase with decreasing productivity, resulting in the higher number of species per unit area observed in low productivity environments. The first component of heterogeneity that we evaluated was the mean semivariogram sill, which is an estimate of the total within-island variation for each island

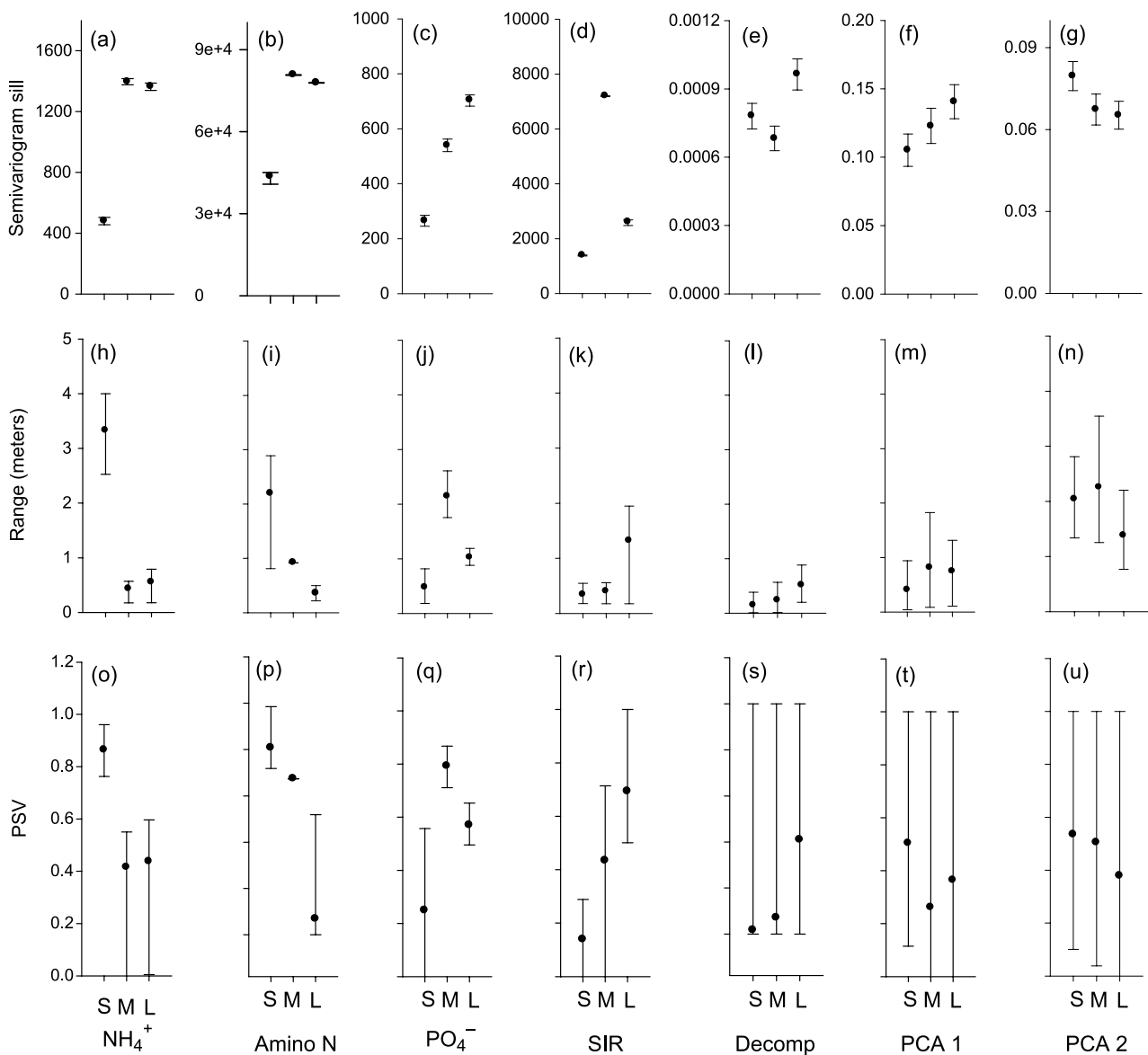


Figure 4. The mean (\pm 95% credible intervals) sill (a–g), range (h–o), and proportional structural variance (PSV) (q–x) for each of three island size classes (small (S), medium (M), and large (L); $n = 10$), of 5 soil variables (NH_4^+ -N, amino N, PO_4^- -P, substrate induced respiration (SIR), and decomposition rate (decomp), and two variables describing plant community composition (principle component analysis (PCA) axes 1 and 2). All means and credible intervals are from posterior parameter estimates obtained from from a hierarchical Bayesian model (see Methods), whereby a best-fitting semivariogram model was used to estimate the mean range, sill and PSV within each island size class for each variable. Means with non-overlapping credible intervals are interpreted as significantly different from each other. For panels (a–g), the sill is an estimate of the sample variance, and therefore the units for each variable are the square of its primary units (panel (a–c), $\mu\text{g g}^{-1}$; panel (d), $\mu\text{g CO}_2 \text{g}^{-1} \text{h}^{-1}$; panel (e), % mass loss; whereas panel (f) and (g) are derived from PCA axes, and are therefore unitless).

size class. For all five soil variables, small islands had a significantly lower mean sill than did large islands, which was inconsistent with our first hypothesis. However, the data also showed that both NH_4^+ -N and amino N demonstrated both a larger range, and a higher proportional structural variance (PSV) on small islands than on large islands, which was consistent with our first hypothesis. This means that despite there being less total variation within small islands, these two available N forms were spatially organized into coarser and more strongly defined patches, whereas on medium and large islands a greater portion of total variation was dispersed randomly across space. Avail-

able soil N is considered to be the primary limiting nutrient in boreal forests (Vitousek and Howarth 1991), and its limitation has been shown to become stronger with successional age and retrogression in this and other boreal systems (Wardle et al. 1997, Schimel et al. 1998, Bond-Lamberty et al. 2006). As such, our finding is consistent with predictions that the most limiting soil resources should exhibit the greatest spatial patchiness (Huston and DeAngelis 1994).

A second goal of our study was to test whether a positive relationship between whole plot variability and species richness was present across islands, as predicted by our

Table 1. A comparison of mean (\pm SE) partial Mantel coefficients for three island size classes (small, medium, and large). The partial Mantel coefficients compare the correlation of a matrix describing dissimilarity in plant community composition with a dissimilarity matrix of five soil variables (NH_4^+ -N, amino N, PO_4^- -P, substrate induced respiration (SIR), and decomposition rate), and a soil matrix describing the multivariate dissimilarity of these soil variables. Data were collected at 49 sampling points collected on each of 30 islands for each variable, with the 10 islands within each size class serving as the units of replication.

	Small islands		Medium islands		Large islands		Island class comparison	
	Mantel	¹ p-value	Mantel	¹ p-value	Mantel	¹ p-value	F-value	p-value
NH_4^+	0.04(0.02)	0.38	0.00(0.02)	0.48	0.03(0.03)	0.41	0.926	0.408
Amino N	0.05(0.06)	0.27	0.00(0.01)	0.47	0.05(0.03)	0.32	1.967	0.160
PO_4^-	0.02(0.03)	0.45	0.05(0.02)	0.30	0.01(0.02)	0.47	0.910	0.414
SIR	0.03(0.02)	0.37	0.02(0.02)	0.40	0.03(0.07)	0.34	0.036	0.965
Decomposition	0.01(0.03)	0.46	0.02(0.02)	0.37	0.02(0.02)	0.43	0.074	0.929
Multivariate soil	0.05(0.02)	0.25	0.01(0.02)	0.44	0.05(0.03)	0.31	1.372	0.271

¹The mean p-value derived from 10 individual Mantel coefficients within each island size class.

second hypothesis. The data showed that neither the whole-plot SD nor the whole-plot CV were correlated with species richness across the thirty islands, thus failing to support our second hypothesis. These results are inconsistent with a number of studies that have shown a positive relationship between resource heterogeneity and diversity (Fitter 1982, Inouye and Tilman 1995, Nichols et al. 1998, Lundholm and Larson 2003, Gundale et al. 2006), but are consistent with others that have not (Collins and Wein 1998, Henry et al. 2002, Baer et al. 2004, Reynolds et al. 2007). One factor that may explain whether or not such a relationship occurs is the magnitude of spatial heterogeneity present, as well as the underlying factors that cause heterogeneity. Many studies that have demonstrated positive diversity–heterogeneity relationships have occurred in study systems that have a high degree of geologic (Nichols et al. 1998, Lundholm and Larson 2003) or topographic (Fitter 1982, Vivian-Smith 1997, Hofer et al. 2008) heterogeneity, or exhibit extreme heterogeneity as a result of recent disturbance (Gundale et al. 2006). In contrast, studies that have failed to find diversity–heterogeneity relationships have often been conducted in systems that are inherently more homogeneous in terms of underlying geology or topography (Henry et al. 2002, Baer et al. 2004, Reynolds et al. 2007, Lundholm 2009), such as is the case in this study system.

Even when there is no relationship between whole plot variability of soil resources and species richness, this does not necessarily preclude heterogeneity from being of relatively greater importance in promoting richness in low productivity environments (Huston and DeAngelis 1994). We directly addressed this possibility through our third hypothesis, which predicted that plant community composition within plots would on average be more strongly correlated with soil variables within small island plots than within large island plots. However, this hypothesis was unsupported by our data; mean partial Mantel coefficients testing for within-plot correlations between soil variables and plant community composition were never significantly different than zero. Significant within-plot soil and plant community correlations were also absent when the first and second PCA axes were used for partial Mantel tests, which isolated the influence of dominant vascular plants and bryophytes in the system (data not presented). This strongly suggests that spatial variation in plant community composition is not coupled to soil resource heterogeneity for any of the island size classes within the study system. Further,

mean partial Mantel coefficients did not show any differences in the strength of these correlations across island size classes. These results are inconsistent with theories that suggest soil resource heterogeneity should be more strongly coupled to variation in species composition in low productivity environments (Tilman 1982, Tilman and Pacala 1993, Huston and DeAngelis 1994).

Given the limited support that our data provide for the role of soil resource heterogeneity in regulating the regional productivity–diversity relationship, and the robust sampling design used to investigate the presence of this relationship, it appears likely that other mechanisms are driving the productivity–diversity relationship at the across-island scale in this study system. One potential mechanism is that islands simply accumulate more species with increasing time since disturbance due to stochastic re-colonization of islands (Myers and Harms 2009). However, this mechanism is unlikely for three reasons. First, all islands are relatively close to mainland communities (maximum distance 3.3 km) (Jonsson et al. 2009); second, islands have all experienced a relatively long period of development since disturbance (i.e. >60 yr); and finally because all plant species can be found on even the smallest and most isolated islands. Therefore species richness per unit area on islands is primarily influenced by the relative abundance of each species within islands rather than the presence or absence of species on islands. An additional mechanism that may influence species richness per unit area across the gradient is the intensity of competition within local communities (i.e. within islands). Some theories that aim to explain the relationship between species richness and productivity propose that species richness in local neighborhoods is determined by the intensity of competitive interactions (Abrams 1995, Grace 1999). Such theories predict that high resource availability leads to lower richness because those species with the highest growth rates (Huston 1979) or highest resource acquisition capacities competitively exclude weaker competitors when resource availability is high (Grime 1979, Huston 1979, Grace 1999). Previous studies from this island system have used a species removal experimental approach to show that competitive interactions among dominant understory species are stronger on large than on small islands (Wardle and Zackrisson 2005), and that dominant plant species exclude colonizing species more on large islands than on small islands (Wardle et al. 2008b).

Our data describing the spatial variability of plant community composition across the island gradient through the use of PCA scores provide some additional support that competition intensity may contribute to the observed productivity–richness relationship in this study system. The first PCA axis, which is driven primarily by spatial variation in cover between the two most abundant understory shrub species within the system (*V. myrtillus* and *V. vitis-idaea*), was more spatially variable on large than on small islands (Fig. 4f). This suggests that, at least at the scale of the 5 cm diameter subplots, these two species are less able to coexist on large islands, which may be a consequence of more intense competitive interactions between them. This is consistent with previous removal experiments in this system which showed that competitive effects of *Vaccinium* species were stronger on larger islands where they are the most abundant (Wardle and Zackrisson 2005). The second PCA axis, which reflects spatial variation in cover between *Vaccinium* species and several less abundant species, demonstrated less spatial variability on large islands relative to small islands (Fig. 4g). The lower variation of PCA axis 2 scores within large islands is explained by the limited presence of rare species that may result from competitive suppression by *Vaccinium* species in these relatively productive environments. Conversely, the higher spatial variability of PCA axis 2 scores on small islands suggests that microsites (i.e. 5 cm plots) are occupied by either the two *Vaccinium* species or by other subordinate species. This pattern would arise if the ability of the two *Vaccinium* species to dominate microsites is less on small islands, thus yielding greater opportunities for other species. These results, in combination with those of removal experiments performed on the same islands (Wardle and Zackrisson 2005, Wardle et al. 2008b), provide some evidence that higher rates of competitive exclusion may occur on the more productive larger islands that may contribute to the decline in species diversity per unit area observed as productivity increases.

Conclusions

Our results have several implications. First, our study provides a robust evaluation of the role of resource heterogeneity in determining regional (i.e. across-island) relationships between productivity and diversity. Our data did not support these theories, suggesting that alternative mechanisms regulate species diversity across the productivity gradient in our study system. Second, these results in combination with earlier results from manipulative experiments on these islands (Wardle and Zackrisson 2005, Wardle et al. 2008b) are relevant to ongoing debates about the role of competition in structuring local plant communities across gradients of productivity (Craine 2005), and suggest that variation in the intensity of competitive interactions may be an alternative factor that influences species diversity in this study system. Finally, these results improve our understanding of how species diversity responds to shifts in resource availability during ecosystem succession and retrogression (Gross et al. 1995, Wardle et al. 2008a). As such they show that resource heterogeneity does not consistently increase as retrogression proceeds, but

that despite this, declines in nutrient availability that are well known to occur during retrogression are still associated with increases in plant species diversity.

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