The influence of scale on the relationships among diversity, function, and invasibility

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Abstract

The relationships among biodiversity, ecosystem processes and biological invasions in natural ecosystem remain unclear in spite of considerable research efforts. Given widespread changes in biodiversity due to high rates of local extinctions, increasing levels of human-induced biological invasions, and dramatic modification of ecosystem processes, understanding the relationships among these factors is critical for developing a predictive understanding of how ecosystems will respond to such changes. To address these issues, I examined patterns in the variance and covariance among understory plant biodiversity, productivity, and decomposition as key ecosystem processes, and the abundance of exotic invasive species in a deciduous forest in Orange County, NY, USA. I also examined how these relationships are affected by five environmental co-variates: (1) soil moisture, (2 and 3) O and A horizon depths, and light availability as measured by (4 and 5) leaf area index and canopy openness. To determine if these patterns were robust across different scales, I examined these relationships at two scales of ecological association: (1) across all understory subsystem types present in the study site, and (2) within two understory subsystem types (seep and mesic). Productivity, decomposition, and invasibility all exhibited scale-dependent patterns. Productivity was correlated with plant species richness, soil moisture, and light availability at the across-subsystem scale, while within both seep and mesic subsystems, evidence points to possible control of ecosystem function by understory plant species richness and functional group richness, but no direct functional influence of the five environmental variables. Decomposition was not related to any measured biotic or abiotic factor across subsystems or within the seep subsystem, yet was explained by plant species and functional group richness in the mesic subsystem. Abundance of invasive species was correlated with productivity, species richness, soil moisture, and light availability across subsystems. While invasive species abundance remained correlated with productivity and soil moisture within the seep subsystem, invader abundance was not related to species richness. These results suggest that the relationships among plant species and functional group richness, ecosystem function, and invasions vary across scales as the influence of environmental factors changes across those scales. Predicting ecosystem response to anthropogenic impacts such as biodiversity loss, alteration of ecosystem processes, and biological invasions is possible if the influence of environmental factors, such as light and soil moisture, and ecological scale are taken into account.

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Introduction

In natural ecosystems, biodiversity, ecosystem processes, and biological invasions vary over space and time in predictable ways (Loreau *et al.*, 2002). That is, the correlative or statistical relationships among these factors are often significant. Increasing human domination and alteration of ecosystems, however, is altering biodiversity, ecosystem function, and invasions, which begs the question as to whether the relationships among these variables remain the same as in relatively unaffected ecosystems. The mechanistic bases of the relationships among these three factors in natural ecosystems remain unclear and somewhat controversial, in part because studies have often focused either on single scales, or on scales that might be considered inappropriate for the inferences drawn (*e.g.*, inferring landscape-level relationships from empirical studies conducted at small spatial and temporal scales).

While considerable research has recently focused on understanding human impacts on Biodiversity-Ecosystem Function-Invasion (BEFI) relationships, this work has been dominated by studies in microcosms, mesocosms, and grasslands, limiting its broad scale applicability. In this study, I focus on forest understory communities, which are virtually unstudied from a BEFI perspective. For example, little is known regarding the relative importance of biotic and abiotic drivers of forest understory ecosystem processes and properties (where *properties* refers to non-process ecosystem characteristics such as stability and invasibility). In particular, few studies have compared the influence of species richness and composition of understory plants on ecosystem function and biological invasion to the influence of abiotic factors such as light, soil moisture, and edaphic properties.

Understory vegetation in forested ecosystems can be an important driver of ecosystem process rates and properties (Nilsson & Wardle, 2005), yet its significance is often overlooked. Understory plants may impede or facilitate canopy productivity and succession (Benitez-Malvido, 2006), and can play important roles in nutrient cycling (Small & McCarthy, 2005; Chastain *et al.*, 2006), maintenance of soil fertility (Brusse *et al.*, 1996), and carbon refixation (Kondo *et al.*, 2005) and sequestration (Chastain *et al.*, 2006). Understory productivity in boreal forests may be comparable to trees (Nilsson & Wardle, 2005), and ericaceous shrubs have even been proposed as keystone species or ecosystem engineers on account of the consequences of their unique leaf biochemistry on biogeochemical cycling (Mallik, 2003). Invasive understory species may also dramatically influence ecosystem processes. C_4 grasses invading Hawaiian woodlands altered nitrogen cycling by increasing fire frequency (Mack *et al.*, 2001), while Japanese barberry (*Berberis thunbergii*) and Japanese stiltgrass (*Microstegium vimineum*) in the northeastern United States increased soil pH and nitrification rates, and exerted negative and positive effects, respectively, on immobilization of soil nitrogen (Ehrenfeld *et al.*, 2001).

The relationship between biodiversity and ecosystem function often follows a positive, saturating curve (Hooper *et al.*, 2005). Study of the relationship between biodiversity and ecosystem processes has assumed a multitude of forms, with approaches ranging from experimental manipulations of diversity (Naeem *et al.*, 1994; Hooper & Vitousek, 1997; Tilman *et al.*, 1997a; Tilman *et al.*, 2001; Hector *et al.*, 1999), to modeling of biodiversity loss scenarios (Tilman *et al.*, 1997b; Schwartz *et al.*, 2000; Bunker *et al.*, 2005) and observational studies (Wardle *et al.*, 1997; Wardle *et al.*, 1999;

Gilliam, 2002; De Clerck, 2004; Weiher *et al.*, 2004; Grace *et al.*, 2006). There is a growing consensus that biodiversity generally increases ecosystem process rates, that functional diversity tends to be a more important driver than taxonomic diversity, and that diversity effects generally saturate at low species richness compared to levels of diversity in ecological communities (Hooper *et al.*, 2005). Recently, a meta-analysis of experimental studies (Cardinale *et al.*, 2006) found that while diversity tends to enhance ecosystem function, sampling effects prevail over complementarity between species as the primary underlying mechanism for the relationship, but such studies are suggestive at best as they do not test directly the presence or absence of mechanism. Thus, research findings remain largely confirmatory, providing existence for a relationship between biodiversity and ecosystem function, but not clearly identifying what mechanisms drive the relationship.

Like studies of biodiversity and ecosystem functioning, study of the interactions between productivity, diversity, and invasibility have also included a variety of approaches. Interest in the relationship between biodiversity and invasibility began with Elton's (1958) hypothesis that more diverse communities repel invasions by utilizing available resources more completely, an effect that has been documented experimentally (Knops *et al.*, 1999; Naeem *et al.*, 2000; Kennedy *et al.*, 2002). The counter hypothesis that higher species richness facilitates invasion on account of higher habitat heterogeneity, species turnover, and nutrient pulses resulting from species turnover has been supported by observational studies (Stohlgren *et al.*, 2003; Cleland *et al.*, 2004; Stohlgren *et al.*, 2006). Experimental and observational studies have thus largely documented apparently contradictory effects of diversity on invasibility, but there is also some observational evidence that invasive abundance can be lower with higher plant diversity (Cleland *et al.*, 2004), and here too consensus is emerging (Fridley *et al.*, *in press*). A further hypothesis evident in the literature is that invasive species can more readily invade productive habitats, and because more productive habitats tend to have higher species richness, diversity and invasibility become correlated (Stohlgren *et al.*, 1999). Alternatively, high levels of production by non-invasive competitors appear to be able to constrain invasions (Cleland *et al.*, 2004; Levine *et al.*, 2004).

In addition to what existing information provides on the relationships among biodiversity, ecosystem function, and biological invasions, studies paying close attention to ecological scale have engendered caution toward considering patterns robust unless shown to persist at different scales (Wiens & Rotenberry, 1981; Gross *et al.*, 2000; Weiher & Howe, 2003; Anderson *et al.*, 2004). In this study, ecological scale refers to scale of ecological association, usage of which grows from Mittelbach *et al.* (2001). Here, scale of ecological association is the hierarchical or organizational level of a unit in an ecological system, such as a biosphere, biome, landscape, ecosystem, subsystem (of an ecosystem), or community, or a subunit of such a unit. Scale of ecological association may correlate with spatial or temporal extent, but because rates of spatial and temporal turnover vary, such a correlation will not always exist.

The importance of targeting ecological inferences to relevant scales cannot be overemphasized (Huston, 1999; Grand & Mello, 2003), and scaling is highly relevant to the relationships among diversity, ecosystem processes, and exotic species invasions. While much attention has been devoted to the soundness of upward extrapolation from microcosm and other small-scale studies (*e.g.* Lawton, 1996; Carpenter, 1996; Kemp *et* *al.*, 2001; Naeem, 2001), soundness of the converse, scaling downward from large scales (*e.g.*, biomes or multi-year patterns) to processes operating at fine scales (*e.g.*, 1 m^2 plots or intra-annual patterns), has received much less attention in ecology.

Spatial and temporal aspects of ecological scale are often readily quantified and well known to be important for the dynamic properties of ecological systems and rates of biogeochemical processes. However, the hierarchical ecological units of scale (conventionally: individuals, neighborhoods, populations, communities, subsystems, and ecosystems), though often equally important (O'Neill *et al.*, 1986; Allen & Hoekstra, 1990), are more difficult to quantify and less well studied.

When studying BEFI patterns and processes, it may be necessary to sub-divide ecological components into subunits that can be defined objectively or quantitatively, and that do not necessarily conform to temporal or spatial differences, or conventional ecological units. After all, for the most part units of ecological scale are not inviolate entities. Rather, they are often constructions with decidedly poorly-defined boundaries, internal partitions, and internal heterogeneity (spatial and temporal variability) in pattern and process (Tansley, 1935; Grace & Pugesek, 1997). For example, meta-populations can be divided into sub-populations with dynamics that are influenced by processes at the meta-population scale, yet both structure and persistence of a particular sub-population are greatly influenced by dynamics within the sub-population itself (*e.g.,* MacArthur & Wilson, 1967; Fahrig & Merriam, 1994). As in the case of metapopulations, division of habitats into subunits can be important in tailoring studies to the scales at which species 'perceive' their surroundings (Kolasa, 1989; Kolasa & Waltho, 1998), and communities and ecosystems can be divided into subunits that may exhibit relationships that cannot be detected at greater scales of ecological organization. Such an approach accounts for, rather than ignores, the influence of scale of ecological association (*sensu* Mittelbach *et al.*, 2001).

Depending on the scale at which a process occurs, the most insightful ecological inquiry may need to be conducted within subunits of conventional habitat, community, ecosystem, or other boundaries. Such efforts may require inquiry within relatively narrow ranges of habitat, community, or ecosystem variables to insure that heterogeneity does not confound interpretation of results. Another approach is to employ sophisticated multivariate models (Grace & Pugesek, 1997; Weiher *et al.*, 2004; Grace *et al.*, 2006), a promising strategy that should greatly enhance understanding of ecosystem regulation.

Here, I examine the relative importance of biotic and abiotic factors on ecosystem function and exotic plant invasion at two scales of ecological association for the understory of a deciduous forest ecosystem (Figure 1). The forest understory can be considered a subsystem of the forest ecosystem, because it comprises pools of nutrients and energy that are components of the greater forest ecosystem. Two goals motivate this study. First, to separate discrete subsystem types according to prevailing differences in environmental conditions, understory plant communities, and understory subsystem ecosystem variables (the three are distinctly associated at the level of the study site). Second, to analyze the influence of key biotic and abiotic drivers of function and invasion within and across these relatively discrete subsystems. The rationale behind this approach is based on the fact that the most important ecological interactions in the understory, such as competition, facilitation, and resource partitioning, operate largely at fine ecological scales (*i.e.,* at the scale of the subsystem or below).

Methods and Materials

Study Site

The study site at Black Rock Forest, Orange County, New York, USA is a late-aggrading temperate deciduous mesic forest with a canopy dominated by red oak (*Quercus rubra*) and chestnut oak (*Q. prinus*). The site is at the base of the northern slope of Black Rock Mountain, and the elevation of the site ranges from 140–220 m. The study site has been free of large-scale disturbance since the first quarter of the 20th century. Slightly less than half of the study site was mechanically thinned in the mid-20th century, yet thinned areas cannot now be distinguished from un-thinned areas by any measure. Oak basal area is remarkably consistent throughout the study site (Schuster, unpublished data).

Understory plant community – systematic site survey

Understory plant community composition and environmental conditions vary considerably throughout the study site. The understory was sampled across the study site using a systematic survey grid of 200 1 m^2 plots. These plots were nested inside twenty 625 m^2 plots (Figure 2), each with ten 1 m^2 plots separated by 4 m along two transects. The 625 m^2 plots were arranged in a grid distributed vertically and horizontally across the slope, with neighboring plots separated by 50 m. Most of the study site has a mesic hydrological regime (76%) or a hillside seep regime (15%), and a small fraction of the study site (9%) in two of the 625 m^2 plots supports a sub-xeric understory composed of mostly *Vaccinium* and *Gaylussacia* where a thick soil O horizon scarcely conceals granitic bedrock.

Mesic areas. The understory in mesic areas commonly includes high abundance of several sedge species (*Carex* spp.), Christmas fern (*Polystichum acrostichoides*), and two ericaceous shrubs, blueberry (*Vaccinium pallidum*) and huckleberry (*Gaylussacia baccata*).

Seep areas. Hillside seeps are scattered throughout the study site, and have small, highly hydric centers and more extensive moist fringes. Seeps are united floristically by high abundance of facultative and obligate wetland herbs such as *Polygonum* spp., *Galium triflorum, Oxalis dillenii, Pilea pumila,* and the exotic invasive grass *Microstegium vimineum*. Other invasive species were also more abundant and more frequently observed in seeps. For the purposes of this study, seeps were defined *a priori* as areas with consistently moist soil ($\leq$ 30 cm deep), regardless of rainfall levels. Species composition is nested ecologically for the most part, such that a subset (approximately 50%) of the species abundant in seeps was observed in mesic and sub-xeric areas.

Ecological scale. In this study, 'ecological scale' builds herein from the usage in Mittelbach *et al.* (2001), in which ecological scale referred to within versus across communities, *i.e.,* scale of ecological association. In this study the scope of ecological scale encompasses subdivision in accordance with community, ecosystem, and environmental parameters. Specifically, the two ecological scales in the study are within the seep (only edges, not centers of seeps) and mesic subsystems of the understory, and across all subsystems at the level of the study site. The systematic survey plots were used to investigate patterns across subsystems, whereas two plant diversity datasets were used to investigate patterns within the seep and mesic subsystems.

Because the majority of the understory in the study site is composed of mesic and seep edge areas, the study focuses on these two forest understory community/subsystem variants toward the goal of understanding the degree to which the relationships between biotic and abiotic drivers of ecosystem and community processes depend on ecological scale. This approach is justified by the distinct differences observed in understory community, ecosystem, and environmental parameters between the subsystems. The seep subsystem had consistently higher soil moisture, productivity, and canopy leaf area index (LAI), lower canopy cover, shallower soil O horizons, and deeper soil A horizons than the mesic subsystem.

Understory plant community – seep and mesic diversity datasets

The seep and mesic understory plant diversity datasets incorporated all 1 m^2 plots from the systematic survey grid that had at least one species with a minimum of 5 dm^2 cover. Plots that could not be included in the diversity datasets were those in the consistently inundated centers of seeps, and sub-xeric ericaceous areas on very shallow soils. Such plots were rare. Thus, the diversity datasets encompass understory communities at the edges of seeps (seep subsystem diversity dataset), and in mesic areas (mesic subsystem diversity dataset). To obtain a full complement of replicated plots distributed from the highest consistently observed plant species richness to the lowest, random sampling was used to identify additional 1 m^2 plots within the 625 m^2 plots. All 1 m^2 plots were separated by a minimum of 1 m, and the process of plot identification prioritized those with composition similar to that of systematic survey plots and all previously sampled plots. The seep and mesic understory plant diversity data consisted of 31 and 48 plots, respectively.

Plant community variables

Cover of understory plants was visually assessed in 1 m^2 plots, and plant diversity was quantified in terms of taxonomic and functional diversity. Here, taxonomic diversity refers to species-level diversity, while functional diversity refers to the diversity of functional groups (defined below). Two metrics each of taxonomic and functional diversity were used: total species richness, effective species richness, total functional group richness, and effective functional group richness.

Taxonomic diversity. Total species richness includes all occurrences of vascular plant species, regardless of the abundance of a given species in a given plot. Effective species richness was defined as the number of species that each meet or exceed 5 dm^2 cover in a given 1 m^2 plot. The distributions of total and effective species richness in the seep and mesic diversity datasets were representative of the distribution of the respective metric in the study site as whole. In the mesic subsystem dataset, higher total and effective species richness values were somewhat over-represented as compared to mesic areas throughout the study site in the systematic survey, yet the difference was not great and both diversity datasets can be viewed as indicative of the understory in the study site as a whole.

Functional diversity. Paralleling measurement of taxonomic richness, total functional group richness includes all occurrences of vascular plant species, regardless of the abundance of a given functional group in a given plot. Effective functional group richness was defined as the number of functional groups that each meet or exceed 5 dm^2 cover in a given 1 m^2 plot. The functional groups identified were C_3 grasses (12 species), C_4 grasses (1 species), early herbs (5 species), late herbs (13 species), non-seasonal herbs (13 species), evergreen ferns (3 species), late ferns (3 species), rhizomatous sedges (1 species), cespitose sedges (8 species), nitrogen fixers (2 species, including 1 legume), and woody plants (20 species).

Thus, all species and functional groups that attained cover $\geq$ 5 dm^2 in a plot were considered to be are effectively present in the plot, and therefore were included as effective species or functional groups. This method was used to reduce upward bias in diversity metrics attributable to variation in evenness by eliminating from the analysis those species occurrences that upwardly bias measurement of diversity most greatly. The use of effective species and functional group richness was predicated on the basis of four main premises: 1) the assumption that species with less than 5 dm^2 are of essentially no community or ecosystem influence at the scale of a 1 m^2 plot; 2) excluding minor floristic components limits inferences to occurrences of species that reflect at least somewhat vigorous recruitment and establishment into a given understory plot, while ignoring occurrences that indicate a more tenuous existence; 3) this method of downweighting rare species has a clearer interpretation than diversity metrics such as Simpson's or Shannon-Weiner diversity; and 4) the use of effective species richness allows for a definition of effective monoculture, in which there is only one species meeting or exceeding 5 dm^2 cover, which was required to operationalize observational estimation of overyielding in the mesic subsystem.

Taxonomic within-functional group diversity. To investigate taxonomic within-functional group diversity, I calculated the total number of species per functional group, and the number of effective species per effective functional group. These measures were attained by taking the average of the number of total or effective species in, respectively, each functional group or effective functional group in a plot.

Composition. For the purposes of this study, plant community composition types reflect differences in the composition of dominant plant species. Thus, some compositional types have only one dominant species, whereas others have more than one species that are co-dominant, and these differences are indicated accordingly.

Invader species. Six plant species were classed as invader species for the purposes of this study. Of these, Japanese stiltgrass (*Microstegium vimineum*) and Japanese barberry (*Berberis thunbergii*) were the most frequently observed and most abundant, while garlic mustard (*Alliaria petiolata*), multifora rose (*Rosa multiflora*), Japanese honeysuckle (*Lonicera japonica*), and wineberry (*Rubus pheonicolasius*) were minor components of the understory. All of these species are well established in the literature as invasive species in forests of the northeastern United States (Randall & Marinelli, 1996; Rice, 2003).

Use of cover to estimate aboveground productivity

Cover serves as a sound proxy for aboveground productivity in the understory study system, because it is correlated with aboveground biomass at the 1 m^2 plot level. Linear regression demonstrated that $\log_{10}$ cover explained most of the variance in $\log_{10}$ aboveground biomass ($df = 13$; $R^2 = 0.749$; $P < 0.0001$), a trend that strengthened with use of untransformed data. ANOVA of the residuals of linear regressions of $\log_{10}$-transformed cover and biomass did not significantly differ for graminoid, herbaceous, and woody growth forms ($F = 38.87$; $P = 0.124$), in spite of slight overestimation of graminoid biomass, and slight underestimation of woody biomass, as might be expected. The data values with the most influence on the slight differences between groups were the values furthest from the origin, which were least common on the study site because cover values were approximately log-normally distributed. Herbaceous biomass deviated little from the linear estimate.

Transgressive overyielding

Transgressive overyielding was used to test for complementarity between effective species in the mesic subsystem. A sufficient complement of effective monocultures (plots in the field with only one species of cover ≥ 5 dm^2) was identified for the mesic subsystem, but depauperate areas were exceedingly rare in seep areas, precluding testing for transgressive overyielding in the seep subsystem. In the mesic subsystem, effective monocultures were identified for ten of the most common species, for which the number of monocultures is indicated: *Agrostis perennans* (1), *Carex communis* (4), *C. digitalis* (5), *C. laxiflora* (1), *C. pensylvanica* (4), *C. swanii* (1), *Gaylussacia baccata* (2), *Mitchella repens* (1), *Polystichum acrostichoides* (6), and *Vaccinium pallidum* (5). *Carex rosea* was the only common species for which no effective monoculture could be identified, and to facilitate analysis the monoculture value of *C. digitalis* was used. Both species are densely cespitose sedges and *C. digitalis* had the highest monoculture value for all cespitose sedge species. Monocultures could not be identified for the three remaining mesic species that reached 5 dm^2 cover, all of which are tend toward low cover in the mesic subsystem: *Aster divaricatus*, *Berberis thunbergii*, and *Cardamine pensylvanica.*

Transgressive overyielding is said to occur if D_{max},

$$D_{max} = \frac{O_T - \max(M_i)}{\max(M_i)}$$

is positive, where O_T is the observed summed cover for a polyculture, and $\max(M_i)$ is the maximum observed cover value in monoculture of all species in the polyculture. Transgressive overyielding has been employed widely in experimental manipulations of plant diversity, and has been proposed as the 'acid test' for complementarity, because significantly positive D_{max} cannot be produced by selection or sampling effects alone (Loreau & Hector 2001; Hooper & Dukes, 2004). However, because it does not allow for partitioning of complementarity effects from sampling effects in terms of their relative contribution to positive trends in function with diversity, it is likely to be a conservative estimate of the degree to which overyielding is occurring.

The use of D_{max} to assess transgressive overyielding in observational studies entails acknowledgement of assumptions that are of less concern in experimental manipulations of diversity. First, because co-varying environmental factors cannot be held constant, it is assumed that environmental differences do not contribute to whether or not overyielding occurs. Second, it is assumed that the maximum monoculture value obtained for a species is the highest value in the study site. While it would be difficult to fully validate these assumptions, they were both addressed in the study design. The first assumption was addressed by testing for environmental influences on function, and the second by sampling the highest possible number of replicate monocultures for each species.

Decomposition

Decomposition was measured via percent mass loss of red oak (*Q. rubra*) leaf litter. Intact oak leaves were gathered from the ground in one area of the study site, dismembered with scissors, and 3.3 g were placed into a 10 x 10 cm mesh bag that was laid on top of the leaf litter in each 1 m^2 plot. The bags were deposited on July 20, 2006 and retrieved on September 10, providing in total a measure of approximately 7.5 weeks of decomposition.

Environmental variables

Five environmental variables were measured for each 1 m^2 plot in the diversity datasets, and a subset of the systematic survey plots. Canopy openness and 4 ring leaf area index (LAI) (Frazer *et al.*, 1999) were calculated from hemispherical canopy photographs with Gap Light Analyzer, Version 2 (Frazer *et al.*, 1999; Simon Fraser University, Burnaby, BC, Canada and Institute for Ecosystem Studies, Millbrook, NY, USA). Soil O and A horizon depths were measured by visually inspecting the soil profile after inserting a spade immediately next to each plot. Soil moisture was measured at 5 cm depth via conductivity with a Lincoln soil moisture meter (LIC, Lincoln, NE, USA).

Statistical analyses

All statistical analyses were performed with Systat Version 8.0 (Systat Software, Inc., San Jose, CA).

Results

Understory plant diversity and understory subsystem productivity

The relationship between understory plant diversity (species and functional group richness) and productivity (as measured by summed cover values in dm^2 of all species) was always positive and significant, regardless of ecological scale (Figures 3-4; Table 1).

At greater scales, (*i.e.*, across understory subsystems), understory productivity was significantly influenced by soil moisture and measures of canopy light penetration, but at finer scales (*i.e.,* within understory subsystems), there was no correlation (Table 2). Productivity was also positively correlated with LAI and negatively correlated with canopy openness at greater scales, but it seems unlikely that understory plants are more productive under low-light environments. Rather, it is likely that understory light availability is negatively correlated with site fertility due to enhanced growth of trees in more fertile areas. Productivity was not correlated with any environmental variable at finer ecological scales, that is within the seep and mesic subsystems (Table 2).

Diversity-productivity relationships within seep and mesic understory subsystems remained positive and significant whether productivity was analyzed as a function of total or effective species richness, and likewise whether as a function of total or effective functional group richness (Figure 4; Table 1). Within both seep and mesic subsystems, effective species and functional group richness explained less of the variance in cover than total species and functional group richness, but effective species and functional group richness demonstrated greater effect sizes as gauged by linear regression coefficients. Total and effective functional group richness usually explained less of the variance in productivity than their respective taxonomic analogues, but demonstrated greater effect sizes.

The effect sizes in all regressions of productivity on diversity were higher within the seep subsystem than in the mesic subsystem, but goodness of fit did not show any consistent trend (Figure 4; Table 1).

In the mesic subsystem, within-functional group taxonomic richness appeared to enhance productivity, as the total and effective numbers of species per functional group significantly explained the residuals of linear regressions of cover on, respectively, total functional group richness and effective functional group richness (Figure 5; Table 1).

In the seep subsystem, however, the strong correlation between effective species and effective functional group richness in diverse plots created an excessive degree of heteroschedasticity that precluded regressing the residuals from a productivity-effective species richness linear regression on the mean number of effective species per functional group (within-functional group effective taxonomic richness). Therefore, it was impossible to conduct an adequate assessment of the effects of effective within-functional group richness on productivity in seep areas. It is also therefore not surprising that the number of total species per functional group in seep areas failed to explain the residuals from a linear regression of cover on total functional group richness (Figure 5; Table 1), because many of the species occurrences involved are likely to be functionally irrelevant.

The potential significance of plant taxonomic richness within functional groups in the seep subsystem remains unclear.

Transgressive overyielding. In the mesic subsystem, approximately two-thirds of polycultures composed of species found in effective monoculture exhibited transgressive overyielding, as measured by $D_{max} > 0$. When D_{max} values for the full set of tested polycultures were combined, polycultures produced significantly positive D_{max} (Figure 6). This was true whether or not the analysis excluded plots containing *Carex rosea,* the only common species for which no monoculture existed. It is unlikely that the omission of *C. rosea* has skewed the results since the analysis employed the maximum monoculture value for *Carex digitalis,* another densely cespitose sedge that had the highest monoculture value of all cespitose sedges in the study. No trends in D_{max} were apparent with effective species or functional group richness (Figure 7).

Transgressive overyielding of species. D_{max} can be used to assess the capacity of a species to overyield or preclude overyielding in a given polyculture, if (of the species present in the polyculture) that species has the highest cover value when found in monoculture (Figure 8). Essentially, if D_{max} is negative in a polyculture where Species A is the most productive species present (*i.e.,* has highest cover value in monoculture of all species in the polyculture), then Species A is the foremost candidate to have precluded overyielding from occurring through competitive interactions with the other species in the polyculture. Alternatively, if D_{max} is positive, Species A is likely to have overyielded, or at the very least, to have allowed overyielding by other species to occur. Even if D_{max} is positive there is no guarantee that Species A has in fact overyielded, but it is likely that the most productive species present will have had some role in determining whether or not overyielding occurs. Though a crude method, it can be useful to assess patterns of overyielding by species.

Two sedge species had the highest monoculture values only in overyielding polycultures: *Carex digitalis* and *C. communis*. The ericaceous shrub *Vaccinium pallidum* and the fern *Polystichum acrostichoides* had the highest monoculture values primarily, but not exclusively, in polycultures that overyielded (including three plots where both species were present and maximal, two of which overyielded). Only one species appeared to always prevent transgressive overyielding, *Carex pensylvanica*, a competitively dominant rhizomatous sedge.

Understory plant community composition and understory subsystem productivity

Plots with different composition of dominant plant species exhibited widely divergent levels of productivity (Figure 9; Table 1). In mesic areas, 6 species composition types, each with 4 or more replicates, were used in ANOVA. In seep areas, the only 3 species composition types with 4 or more replicates each were used in ANOVA. The compositional uniqueness of the most diverse plots, *i.e.*, on account of unique combinations of dominant species, precluded their inclusion in ANOVAs in both the seep and mesic subsystems.

In the mesic subsystem, composition types with 4 or more replicates differed significantly in an ANOVA on their effects on understory subsystem productivity in the mesic subsystem. Least Significant Difference post-hoc tests demonstrated that plots dominated by the rhizomatous sedge *Carex pensylvanica* had significantly higher cover than plots dominated by the cespitose sedges *Carex communis* or *C. digitalis,* the fern

Polystichum acrostichoides, and the ericaceous shrub *Vaccinium pallidum.* No other post-hoc comparisons pointed to significant differences.

In the seep subsystem, composition types with 4 or more replicates differed significantly in their effects on understory subsystem productivity. LSD post-hoc tests demonstrated that plots unified by co-dominants *Microstegium vimineum* and *Pilea pumila* (an exotic invasive C_4 grass and a native dicotyledonous herb, respectively) had significantly higher cover than plots dominated by *C. pensylvanica,* and from those co-dominated by *C. digitalis* and 1+ other *Carex* species. No post-hoc difference was observed between the two *Carex*-dominated composition types.

Understory plant diversity, composition and understory subsystem decomposition

Mass loss of red oak leaves exhibited a different form of ecological scale-dependence than productivity. Decomposition rate, as measured by percent mass loss of red oak leaf litter, showed no relationship with total plant species richness, productivity (Figure 10; Table 1), soil moisture, canopy openness, or LAI across subsystems (Table 2).

Similarly, within the seep understory subsystem, no measure of plant taxonomic (Figure 11; Table 1) or functional group richness exerted any detectable influence on oak leaf percent mass loss, nor was decomposition related to any measured environmental variable (Table 2), precluding interpretation of what may drive decomposition in seep zones. Decomposition was faster in seep areas than in mesic areas (data not presented) presumably on account of higher moisture, but soil moisture measurements could not explain this pattern.

In contrast, understory plant species and functional group richness influenced decomposition within the mesic understory subsystem, although always weakly (Figure 11; Table 1), while environmental factors again failed to explain decomposition rate (Table 2). Both total and effective species richness appeared to accelerate mass loss, as did total functional group richness. Effective functional group richness exerted a marginally insignificant effect. Unlike for understory productivity, total and effective species richness, and total and effective functional group richness explained roughly similar amounts of the variance in percent mass loss. Nonetheless, effective species richness explained more variance than total species richness, and the effect size for total functional group richness was higher than for total species richness. Because percent mass loss is a net measure that does not account for accumulation of microbial biomass – which may well be highest when decomposition is maximal – effect sizes of percent mass loss estimates might be considered conservative.

In both understory subsystems, the identity of the dominant species (*i.e.*, species composition) showed no effect on percent mass loss of oak leaf litter (Figure 12).

Understory plant diversity, productivity, and exotic species invasion

Cover of exotic invasive species was significantly positively correlated with total understory plant species richness, productivity (Figure 13; Table 1), and soil moisture (Table 2) across all understory subsystems. As for productivity, invasive cover was positively correlated with LAI and negatively correlated with canopy openness, but again the effect here appears to be a negative correlation between light availability and habitat fertility.

The site-level, across-subsystem correlation of invasibility with species richness was dependent on ecological scale, and can be accounted for by differences in invasibility across subsystems. While invasive species cover remained correlated with productivity (Figure 14; Table 1) and soil moisture (Table 2) within the seep subsystem, there was no such correlation between invasive species cover and either total or effective species richness (Figure 14; Table 1).

Invasive species appear to have more readily colonized and invaded wetter, more fertile habitats, whether viewed at the across-subsystem or within-seep subsystem scales. Because the within-subsystem ecological scale does not aggregate environmental heterogeneity relevant to fine-scale community processes such as competition and facilitation that presumably structure interactions between exotic invasives and non-invasive plants, the association between species richness and invasibility at the across-subsystem scale appears to be attributable to variation in site fertility.

Environment, understory plant diversity, and understory subsystem function

Understory productivity and percent litter mass loss appear to exhibit scale-dependent influence of environmental conditions. Across subsystems, productivity was correlated with soil moisture and negatively correlated with light availability, while decomposition was not correlated with any of five potentially important environmental variables: soil moisture, percent canopy openness, canopy LAI, soil O horizon depth, and soil A horizon depth (Table 2).

At within-subsystem scales, no such correlations between environmental factors and ecosystem processes were observed. Therefore, while environmental variation could explain positive relationships between understory plant taxonomic and functional group richness and ecosystem processes at the across-subsystem scale, it could not explain richness-function relationships at within-subsystem scales. These observations stand in marked contrast to the apparently pre-eminent roles of soil moisture and site fertility in altering the potential for biological invasions both across subsystems and within the seep subsystem.

Plant species richness was at times positively correlated with site fertility at within-subsystem scales. In seep areas, total species richness was marginally insignificantly correlated with canopy leaf area index, and in mesic areas, effective species richness was significantly correlated with soil A horizon depth (Table 2). Because each of these environmental factors were correlated with some measure of plant diversity but were uncorrelated with productivity and decomposition, the relationships among the environment, species richness, and ecosystem process rates may suggest that environmental variables influence how many species can co-exist in a given location, providing an ecological framework under which understory plant species richness may act as an important driver of the magnitude of productivity and decomposition rates.

Discussion

Understory biotic and abiotic influences on understory subsystem function

BEFI relationships, as outlined in Figure 1, were strongly influenced by the ecological scale at which they were measured. While abiotic environmental conditions influenced plant production (*i.e.*, cover) across understory subsystems (Table 2), plant species richness influenced production within subsystems (Figures 4-5).

In contrast, decomposition showed no signal across understory subsystems and within the seep subsystem for any measured potential causative agent (Figure 10), while plant species richness again emerges as the foremost candidate driver within the mesic subsystem, significantly explaining decomposition of oak leaf litter (Figure 11).

Plant taxonomic and functional group richness appear to be important determinants of ecosystem function in the understory subsystem, for both productivity and decomposition. While plant species composition and richness both accounted for much of the variance in productivity, it remains unclear how the strength of compositional effects on productivity (Figure 9) compares to that of taxonomic and functional group richness. However, the striking lack of signal between species composition and decomposition (Figure 12) demonstrates that understory plant species composition is unlikely to be as significant a driver of decomposition as taxonomic or functional group richness.

These results support the importance of ecological scale in understanding the relative importance of biotic and abiotic drivers of ecosystem process rates. These findings corroborate those of Guo & Berry (1998), who found that species richness-productivity relationships in the Chihuahuan Desert varied dramatically when separated according to habitat types. However, Guo & Berry found relationships varying from positive to negative within habitats, and a unimodal relationship across habitats. The positive diversity-productivity relationships observed at all scales in this study appear to reflect fundamental differences between the Chihuahuan Desert and northeastern deciduous forests, likely attributable to both widely divergent environmental parameters and species pools. Species richness-function relationships also exhibited fairly consistent effect sizes and goodness of fit in linear regressions, regardless of scale or subsystem (Table 1). Guo & Berry did not take the evenness component of diversity into account, as did this study by the use of effective species and functional group richness. It is difficult to predict how much the relationships in Guo & Berry might change if inferences were constrained to species occurrences that are functionally active at the level of the sampling unit.

In mesic areas the ecosystem significance of effective species richness was clear, as evidenced by the significantly non-zero and widespread overyielding (Figure 6). Such results provide evidence for the importance of complementarity between species, though direct, manipulative tests are necessary to confirm that complementarity is indeed the underlying mechanism. The relative contributions of complementarity effects and sampling effects could not be determined in this study (see below), yet the results easily pass the 'acid test' of transgressive overyielding.

Plant species and functional group richness influenced seep subsystem productivity slightly more strongly than in mesic zones (Figure 4), regardless of whether complementarity or sampling effects are the mechanisms responsible for the effect. Because the rarity of effective monocultures in seep areas precluded calculation of D_{max}, analysis of the implications of species richness for seep productivity could not match the degree of relative clarity attained for mesic productivity. Nonetheless, given that linear regressions between seep species richness and productivity had effect sizes and goodness of fit comparable to those of mesic areas (Table 1), and given that mesic and seep areas share approximately 50% of their species, seep zones may well support similar levels of complementarity.

Plant species and functional group richness in mesic areas influenced decomposition rate, although the relationship was fairly noisy (Figure 11). This variability may result from the peculiarities of using net percent mass loss to measure decomposition, namely that accumulation of microbial biomass is unaccounted for, and may be greater in more rapidly decomposing litter. Given that mass loss may thus be rendered a conservative estimate of decomposition, an important step toward understanding diversity-decomposition effects will be to correct measures of decomposition for microbial biomass or abundance.

It is noteworthy that the linear regression estimates for dependence of decomposition on total and effective species richness were more robust (*i.e.*, higher R^2; Table 1) than for cover, which may indicate that species richness influences decomposition rate over and above the contribution of species richness to enhanced subsystem productivity. If species richness influences are not limited to indirect effects through increased production, it remains unclear what mechanism is responsible.

It seems possible that deposition of superior-quality litter of understory plants in a mesic litter layer of mostly inferior-quality oak litter could ameliorate nitrogen and other nutrient deficits for microbes active in decomposition. This mechanism appears somewhat unlikely, considering how inconsistently mass loss varied across the broad range in leaf litter chemistry in the community (*i.e.*, the lack of consistent plant species composition effects; Figure 12), and that the relationship with effective functional group richness was weaker than with all other measures of plant diversity (Figure 11).

Nevertheless, if litter of all (or even most) understory plant species accelerate decomposition relative to the predominant substrate of oak litter, decomposition may be affected little by differences in litter quality between understory species. Abiotic conditions could then constrain decomposition, or perhaps a depauperate species pool of high-quality litter decomposers on account of the isolation of diverse understory plant assemblages in a veritable sea of oak leaf litter. This could be especially true if all understory species amend the bacterial-based soil energy channel, enhancing decomposition by effectively adding an entire energy channel to the almost certainly fungal-based channel dominating utilization of inferior-quality oak leaf litter (Wardle, 2005), and thereby creating greater potential for activity and synergy among decomposer micro- and macro-flora and fauna.

In seep areas the lack of a discernable influence of any potential biotic or abiotic driver of percent mass loss (Figure 11) suggests that decomposition is not affected by these factors. Perhaps the consistent moisture in seeps leads decomposition rates to fluctuate as over time they are alternately stimulated by moderate soil moisture and retarded by inundation. Alternatively, decomposition in seep areas may be limited by unmeasured abiotic or biotic variables such as temperature or soil microbial community structure, and any such factor would appear to be more important than any influence emanating from the plant community under the seep environmental regime.

Correlation of productivity and decomposition with environmental variables could not explain within-subsystem diversity-function relationships, despite across-subsystem correlation between environmental conditions and productivity (Table 2). Thus, while environmental measurements appeared sufficiently precise to witness effects on ecosystem processes, environmental variables did not prove important when inferences were restricted to diversity-function relationships within the seep and mesic understory subsystems. The absence of an alternative environmental explanation for trends in diversity and function does not support the notion that such relationships are simply the product of confounding environmental variation, and provides a level of confidence that the results accurately reflect legitimate influences of species and functional group richness on process rates.

Taken together, the results of the study support the hypothesis that reductions in understory plant taxonomic and functional group richness would reduce ecosystem process rates in these forest understory subsystems. Although the effect of local extinctions on ecosystem function would be subject to the peculiarities of the specific driver or drivers causing attrition of diversity, the evidence presented here supports the conclusion that retaining understory plant taxonomic and functional group richness will go far toward maintaining ecosystem process rates. This may be particularly true in the case of the extreme herbivory by white-tailed deer, *Odocoileus virginianus*, perhaps the most significant threat to understory plant diversity in the study site and throughout northeastern deciduous forests (Russell *et al.*, 2001; Rooney *et al.*, 2002). This factor may interact with another local and regional threat to northeastern forest understory plant diversity, invasion of exotic plant species, yet the effects of invasions on diversity-function relationships are likely to vary with the physiology and ecology of particular invasive species.

The consequences of biodiversity loss ultimately relate to the commonness and rarity of different levels of biodiversity. Total species richness approximates a normal distribution in both seep and mesic areas, whereas seep assemblages show a distinctly flat distribution of effective species richness (kurtosis = -0.674), and effective species richness declines in an exponential manner in mesic assemblages. In the mesic subsystem, under 6% of vegetation in the forest understory supports effective species richness of three or more. Thus, if effective species richness declined in assemblages with effective species richness of three or four, the effect of the loss on function will be virtually negligible at and above the level of the study site. Nonetheless, if these results can be generalized to northeastern deciduous forest ecosystems, there are bound to be areas where diverse assemblages of similar species composition are more common, and where loss of diversity could significantly impair functioning of the subsystem. If species richness declines in seeps, the effects could be substantial in terms of reduction of seep subsystem-level process rates, and could be exacerbated by the high degree of functional group singularity in diverse seep assemblages.

Elton's hypothesis: understory plant diversity, productivity, and invasibility

Invasive species abundance was significantly correlated with total species richness, understory productivity, and environmental parameters at the across-subsystem scale. While the correlations of invasibility with productivity and site fertility were robust to scale of ecological association in the seep subsystem, the relationship between species richness and invasibility disappeared at the within-subsystem scale. This outcome does not explicitly support Elton's hypothesis, but may not contradict it if species richness and productivity exert countervailing forces on invasibility. It is possible that Elton's hypothesis is active in the form of decreasing invasibility as total species richness ranges from medium to high (Figure 14), resulting from higher resistance to invasion above a threshold of moderate total species richness. However, effective species richness demonstrated no such trend (Figure 14), and lower fertility does not appear to explain low abundance of invasive species in species-poor assemblages. To the contrary, canopy LAI showed a positive, marginally insignificant correlation with total species richness (Table 2), suggesting a positive response of canopy trees to greater site fertility where total understory species richness is lower. The overall outcome is to cast uncertainty on the possibility that species richness influenced invasion.

Trends in exotic invasive species abundance with species richness did not support two hypotheses that have accumulated evidence in the ecological literature: Elton's (1958) hypothesis that more diverse communities repel invasions, and the counter hypothesis that higher species richness facilitates invasion (Stohlgren *et al.*, 2003; Stohlgren *et al.*, 2006). The results provide support for a third hypothesis, that invasive species favor more productive sites, which tend to sustain high species richness (Stohlgren *et al.*, 1999), downgrading widely observed large-scale relationships between species richness and invasion from causality to correlation. This observation stands in contrast, however, with observations that productivity may constrain invasibility (Cleland *et al.*, 2004).

These results may suggest that experimental studies documenting resistance to invasion through plant diversity (Knops *et al.*, 1999; Naeem *et al.*, 2000; Kennedy *et al.*, 2002) have identified a mechanism in nature that may be influenced by a variety of factors. The diversity-invasibility relationship may depend on environmental conditions, community composition, functional diversity, the nature of competitive and facilitative interactions among the species in a community, or some combination of these factors. For example, the effectiveness of the mechanism in which communities with high native diversity draw down resources more than less diverse communities, thereby inhibiting establishment of invaders, may depend on the resource use patterns of the species in a community. If diverse assemblages consist of coexisting of plant species that are effective competitors for different limiting resources, it is possible that resource draw-down may not vary much with changes in species richness, entailing that the inhibition of invasion may not necessarily be associated with species richness.

Ecological scale, biodiversity, and ecosystem function

Several authors have critiqued experimental evidence that biodiversity positively influences productivity by suggesting conflict with an extensive body of empirical ecological literature that provides support for species richness being a unimodal function of productivity (reviewed in Waide *et al.*, 1999; Mittelbach *et al.*, 2001), generally referred to as the hump-shaped model (*sensu* Grime, 1973). The primary underlying theoretical basis for this empirical phenomenon is that few species can exist in unproductive habitats, while species richness increases as environmental constraints are ameliorated in more fertile habitats, yet species richness declines in highly fertile habitats as competitively subordinate species are competitively excluded by superior competitors. However, some empirical studies have not considered the potential influence of ecological heterogeneity on the biodiversity-productivity relationship.

In the studies reviewed by Waide *et al.* (1999) and Mittelbach *et al.* (2001), trends at local scales typically took the form of hump-shaped curves, yet studies at local scales were defined as having a spatial extent of < 20 km. This criterion does not provide for an adequate test at the fine scales that should be most relevant to diversity-function relationships, especially if confounding ecological heterogeneity is not accounted for. While Waide *et al.* and Mittelbach *et al.* distinguish between studies within- and across-community studies to examine effects of scale of ecological association, resolving the influence of scale requires more detailed analysis.

Insufficient attention to confounding heterogeneity is perhaps most clearly demonstrated by the archipelago study of Wardle *et al.* (1997), which analyzed correlations among plant composition and species richness, fire frequency, and several ecosystem properties across islands of varying size. The high degree of potential for confounding correlation among collinear drivers has the effect of clouding the conclusion that plant species richness did not influence ecosystem process rates, requiring statistical partitioning of confounding variables (Tilman *et al.*, 1997c) and a tremendous degree of replication. In the island study system, a rigorous test of the influence of plant species richness on ecosystem processes would involve intensive study of relationships within islands, with patterns between islands relegated to a component of the study rather than the central analysis, or alternatively multivariate modeling such as path analysis.

One of the primary criticisms of experimental studies that emanates from the logic of the hump-shaped curve is that competitive exclusion in highly fertile habitats results in low species richness, while productivity and perhaps other process rates are maintained. This criticism is related to possible dominance of sampling effects over complementarity or ecological interactions such as facilitation, where sampling refers to productive dominant species controlling function. More recently, studies have demonstrated that competitively superior species can overyield even more strongly than less competitive species (Roscher *et al.*, 2005), and while the current study provides evidence that productive species may exert influence that is important at the plot level, there was no evidence for the influence of productive competitive species at the ecological scale of the mesic subsystem.

The competitively dominant sedge *Carex pensylvanica* was the only species that clearly failed to produce transgressive overyielding in mesic areas, providing no evidence for the operation of complementarity effects in the polycultures that contained *C. pensylvanica*. This observation is in agreement with studies that have documented the competitive superiority of *C. pensylvanica* (Abrams & Dickmann, 1982; Folgate & Scheiner, 1992; Nielson *et al.*, 2003). However, this species appeared to have had little effect on the overall trends of increasing productivity with species and functional group richness, and widespread transgressive overyielding in the mesic subsystem.

Given the above, when the biology of such a species clearly conforms to the predictions of the hump-shaped model, the question of what generates the conflict between the predictions of the hump-shaped model and empirical evidence apparently to the contrary is misplaced. In reality, no such conflict exists. The model correctly predicts the ecosystem consequences of *C. pensylvanica,* but mitigating factors attributable to the structure of this natural ecosystem reduce its impact on process rates.

It is important to recognize that the relationship between species richness and productivity is far from deterministic (Mittelbach *et al.*, 2001), and as the results here demonstrate, may depend on the degree of representation of competitive dominants in the community. *C. pensylvanica* is a rhizomatous sedge that is found in clonal patches spaced widely throughout the study site, and is therefore absent from the vast majority of mesic areas (only 4% of mesic areas support *C. pensylvanica* at $\geq$ 15% of 1 m^2 plot cover, and very rarely at $\geq$ 50%). All other species common in the mesic subsystem either overyielded consistently, or at the very least demonstrated the capacity for transgressive overyielding (Figure 9) (although rarer still than *C. pensylvanica,* the fern *Dennstaedtia punctilobula* was another productive species with the potential for high dominance).

If competitive dominants that inhibit overyielding account for few species and few species occurrences in a community, it appears unlikely that 1) the species will contribute to sampling effects responsible for a positive correlation between species richness and process rates, and that 2) strong competitive dominance manifested along the high-productivity downward slope of the hump-shaped curve will be prevalent enough to exert an overwhelming degree of control over process rates, at least above the plot scale. It is also noteworthy that *C. pensylvanica* abundance in monoculture often fell well below the maximum monoculture value used to test for transgressive overyielding; here the conservatism of transgressive overyielding as a test for complementarity must be considered.

An additional observation regarding *C. pensylvanica* and sampling effects is that the species was rarely found in diverse plots. In fact, it was the only common mesic species for which more monocultures were sampled than polycultures. In essence, not only is the species an effective competitor, it is so effective that it has little potential to increase productivity through sampling effects in polycultures. When the infrequent occurrence of *C. pensylvanica* in diverse polycultures is combined with the probable irrelevance of the species in terms of process rates at scales greater than the plot scale, it is not surprising that this species seems to have insignificantly affected relationships between species and functional group richness and function. Together, these observations regarding *C. pensylvanica* not only suggest that studies of diversity and function should pay greater attention to the prevalence of productive competitive dominants in communities, and that unimodal trends in species richness with productivity may be more common when such species are better represented, but also that sampling effects contributing to positive species richness-function relationships may be uncommon if productive competitive dominants rarely occur in diverse assemblages.

Ecological scale, biodiversity, productivity, and biological invasions

In this study, the correlation between plant species richness and invasibility was dependent on scale of ecological association, because it was only evident across subsystems, and not within subsystems. Because apparent influences of habitat fertility on invasions were robust to scale, the across-subsystem correlation of species richness and invasibility appears to be attributable to variation in habitat fertility rather than plant species richness.

The results furthermore indicate that regional and continental analyses have not adequately tested whether species-rich communities are more easily invaded at neighborhood and plot scales, despite claims to the contrary (Stohlgren *et al.*, 2003). Even if data are collected at fine spatial scales, this form of analysis effectively tests correlations between species richness and invasibility only across habitats (or at still greater scales), which cannot be reconciled with the stated goal of testing for invasibility at neighborhood-to-plot scales. These massive data sets would only be useful in testing for invasibility patterns at the typically fine scales over which biodiversity-ecosystem interplay occurs if habitat/community/ecosystem influences are incorporated into the analysis.

Research on biodiversity, productivity, and invasibility should benefit from explicit consideration of scale of ecological association, in addition to spatial and temporal grain and extent. The results of this study suggest that environmental and ecosystem effects on site fertility may explain much of the variance in invasibility, and that large-scale studies enable prediction of the invasibility of localities and habitats based on productivity, and perhaps co-varying species richness, but will not enable prediction of what ecological outcomes are likely within localities, nor within habitat, community, and ecosystem subtypes that comprise localities.

Implications for biodiversity-ecosystem function research

The clearest implications from this study for biodiversity and ecosystem function (BEF) research are that resolution of trends in natural ecosystems in accordance with scale of ecological association will greatly improve understanding of the consequences of biodiversity loss, and that some predictions of ecosystem structure effects on BEF relationships may be less important than hypothesized in this system.

There are well-known trade-offs in BEF research associated with observational versus experimental approaches. Synthetic communities have the advantage of directly testing diversity effects, but are likely to experience change in diversity and the diversity-function relationship in the absence of treatment maintenance as the effects of ecological variables deepen over time. Indeed, BEF experiments manipulating plant diversity have often found that the relationship intensifies greatly over time (*e.g.* Tilman *et al.*, 2001; Reich *et al.*, 2001; van Ruijven & Berendse, 2005; Roscher *et al.*, 2005). Perhaps the greatest advantage of observational approaches, though they cannot control co-varying factors, is that they provide for inferences based on information on ecosystem properties and processes that integrates across a rich history of trophic, population, community, ecosystem, and environmental interactions. While past trajectories of different replicates cannot be fully known, and extensive replication is necessary to ameliorate the influence of variability, unplanned variation can provide unexpected insights into interactions in real ecosystems, as in the current study. But perhaps most importantly, by tracking trends through time in real ecosystems, changes in relationships and stability can be assessed in response to perturbations paralleling global change scenarios.

In addition to concerns arising from variability, observational biodiversity-ecosystem function research entails the limitation that estimation of overyielding may be restricted to transgressive overyielding as measured by D_{max}. Here, the data do not meet the assumption of constant final yield by density, prohibiting the use of additive partitioning (Loreau & Hector, 2001; Hooper & Dukes 2004), which separates complementarity effects from sampling effects, and measures the contribution of the two effects to positive influences of diversity on ecosystem function. One of the main issues here is that predicting polyculture yields from monoculture as the reciprocal of species richness cannot be justified. If appropriate expected values could be derived from monocultures in a manner robust to variable density, perhaps complementarity and selection could be teased apart observationally. Another potential limitation in observational BEF studies can be securing sufficient replication of monocultures, as in seep areas for this study, on account of the uncommonness of such depauperate areas in certain natural ecosystems. This is one realm from which removal and *in situ* planting experiments can derive considerable appeal.

In BEF research, observational studies have typically been less favored in comparison to experimental studies over the last decade. Some authors have claimed that observational studies cannot adequately test for ecosystem consequences of biodiversity on account of confounding environmental variation (Roscher *et al.*, 2005), whereas others have relied on insights from both manipulated and intact natural ecosystems (Wardle *et al.*, 1997; Wardle *et al.*, 1999; Smith and Knapp, 2003; De Clerck, 2004). Removal experiments have proven particularly effective in examining relationships between species richness and ecosystem processes (Wardle *et al.*, 1999; Smith and Knapp, 2003), although they carry their own limitations (Díaz *et al.*, 2003). Thus, each method has well-known advantages and limitations, but in combination they can provide the greatest breadth of insight into BEF relationships than any one method alone. This observational study augments the growing body of diverse literature on BEF research.

The other primary contribution of the present study to BEF research is that it provides alternative explanations for certain predicted influences of ecosystem structure on BEF relationships that are related to the consequences of the dominance of productive species in natural ecosystems. The expected result of dominance in natural ecosystems is to introduce sampling effects that are responsible for any positive relationship between species richness and function, and because most communities are assumed to support high dominance, sampling effects are suggested to often be the pre-eminent driver of positive diversity-function relationships observed in natural ecosystems (Schwartz *et al.*, 2000).

For dominance to induce sampling effects, two inherent additional assumptions must be met, namely that productive competitive dominant species are abundant, and that such species are also found in diverse assemblages. The influence of the often highly dominant, productive, and competitive species *Carex pensylvanica* on the species richness-function relationship appeared to be minimal at the scale of the mesic understory subsystem. Because the species is absent from most of the study site and is rarely found in diverse assemblages, it did not prevent transgressive overyielding from being prevalent, and appears to have contributed little in terms of sampling effects to the positive species richness-function relationship. Therefore, the necessary assumptions were not met in order for dominance to exert overwhelming influence on the relationship between species richness and function. The inability to employ additive partitioning of sampling and complementarity effects entails incomplete knowledge regarding the strength of these mechanisms, yet the evidence for widespread transgressive overyielding provides consistent evidence for niche complementarity effects in spite of the presence of productive competitive species in the system.

Taxonomic and functional understory plant diversity

The use of effective species richness and effective functional group richness provided important insights into BEFI relationships. Effective richness tended to show stronger functional relationships than total richness, or showed relationships when total richness showed no relationship at all. This trend of greater apparent sensitivity appears to be due to the ability of effective richness to account for bias attributable to variation in evenness (bias resulting from the least abundant species in a given plot). In this study only species and functional groups with less than 5 dm^2, the minimum cover that was considered to be conceivably consequential at the scale of a 1 m^2 plot, were excluded from effective species richness.

The ecological information conveyed by measures of effective richness might be considered more accurate than measures of absolute richness, because it only includes occurrences of species and functional groups that reflect successful recruitment and establishment into the understory sampled in a given plot. Because the use of effective richness is an attempt to include only conceivably functionally important species and functional group occurrences, it is a step toward eliminating the concern that species and functional group occurrences that are irrelevant in terms of function have any significant bearing on analysis of diversity-function relationships. It also eliminates the need to seek rare monocultures of species that occur at very low densities. 5 dm^2 per 1 m^2 plot is an arbitrary cutoff point however, and assumes that occurrences below this threshold are indeed of little consequence functionally. It would be useful to identify the minimum absolute abundance for a species or functional group to affect processes or properties in a plot of a given size, or to demonstrate a consistent response to plot-level ecological phenomena. This information would also go far toward ensuring that all species of true functional consequence are included in overyielding calculations. Using a minimum value should prevent loss of minor but functionally consequential species and functional groups occurrences, ensuring that all functionally significant occurrences are included in analyses.

Effective taxonomic and functional group richness tended to exhibit greater effect sizes in diversity-function trends, and in the mesic subsystem showed saturating effects of effective species richness, and a correlation with soil A horizon depth. These observations suggest that studies including potentially functionally irrelevant species occurrences in measurement of diversity may be missing trends driven solely by species of functional importance. For instance, recent studies have employed rigorous multivariate observational analyses of biotic and abiotic influences on ecosystem processes in grasslands (Weiher *et al.*, 2004; Grace *et al.* 2006), and concluded that species richness was of little to no functional consequence. Yet neither of these studies considered the functional potential of species occurrences, *i.e.* some combination of richness and evenness, and therefore the power to detect patterns attributable to plant diversity is likely to be reduced. It should also be noted that these two studies did not incorporate functional diversity, which this study, among many others, suggests may reduce the strength of apparent biodiversity influences on function.

While diversity and evenness indices are not easily interpretable in terms of ecosystem significance, and are difficult to compare across ecosystems and scales, effective species and functional group richness metrics are efficacious, tractable, and permit clear interpretation. Though not a panacea for comparisons across systems, they can be defined with objective criteria appropriate for the systems, scales, organisms, and processes of inquiry.

Synthesis

Taken together, the results suggest that efforts to understand the relationships among biodiversity, ecosystem processes, and invasibility can benefit from examining environmental, community, and ecosystem variation of natural systems. Observational BEFI studies, in particular, can benefit from incorporating evenness into their analyses of diversity effects. Furthermore, the lack of evidence for some hypothesized consequences of productive competitive species on BEFI relationships in natural ecosystems support the potential importance of biodiversity influences on function in the world's ecosystems.

Enhanced efforts devoted to examining ecological scale can contribute to reducing the influence of factors that can confound study of BEFI relationships. The existence of subunits or intergrading internal variability within conventional hierarchical levels of ecological organization entails that conventional ecological levels are often not truly discrete, and that analysis at these levels may not necessarily avoid confounding ecological heterogeneity. Resolution of BEFI relationships will benefit from more studies of natural ecosystems that match scales of inquiry with the scales at which mechanisms operate; this is a fact well known by ecologists, but missed in several recent BEFI studies.

These results illustrate the possible role of ecological heterogeneity in confounding the interpretation of observational data taken from large-scale studies, as well as the importance of scale of ecological association in determining the nature and magnitude of biotic and abiotic influences on ecosystem process rates and exotic species invasions. It should be particularly informative to conduct studies that analyze the role of scale of ecological association in conjunction with more conventional treatment of spatial and temporal grain and extent.

The hypothesis that dominant productive species are abundant and drive positive biodiversity-function relationships (*i.e.,* the sampling effect), was not supported here. Although it was not possible to test for the relative strength of sampling and complementarity effects, widespread transgressive overyielding supported the operation of niche complementarity in the context of the ecosystem structure of mesic areas, and moreover there was no evidence supporting overwhelming influence of dominance.

Finally, incorporating information on evenness into studies of the ecosystem and community importance of diversity provides an important step forward, and culling functionally inconsequential species and functional groups from data is one approach toward this goal.

Understanding the relationships among biodiversity, ecosystem function, and biological invasions in natural ecosystems, and how ecological scale influences these relationships, is important for improving the predictive capabilities of ecology. Studies that improve the predictability of ecology will facilitate human stewardship of biodiversity and ecosystem services.

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Tables and Figures

Table 1. Summary statistics from linear regressions and ANOVAs for diversity, ecosystem function, and invasibility.

Understory plant diversity, composition and understory subsystem productivity

Subsystem, scale	Independent Variable (transformation)	Dependent Variable (transformation)	R^2	Inter-cept	Coeff.	F	*P*	N	df
All, across subsystems	Total species richness	Cover (log)	0.409	0.49	0.12	119.68	< 0.0001	175	173
Seep, within subsystem	Total species richness	Cover (log)	0.410	1.70	0.03	20.12	< 0.0001	31	29
Seep, within subsystem	Effective species richness	Cover (log)	0.525	1.67	0.07	32.10	< 0.0001	31	29
Seep, within subsystem	Functional group richness	Cover (log)	0.537	1.48	0.10	33.61	< 0.0001	31	29
Seep, within subsystem	Effective functional group richness	Cover (log)	0.392	1.66	0.10	18.74	< 0.0001	31	29
Seep, within subsystem	Total species per functional group	Residuals of Total functional group richness - Cover (log)	0.000	0.01	0.04	0.01	0.914	31	29
Seep, within subsystem	Composition	Cover (log)	0.697			10.36	0.005	12	9
Mesic, within subsystem	Total species richness	Cover (log)	0.552	0.92	0.09	56.57	< 0.0001	48	46
Mesic, within subsystem	Effective species richness	Cover (log)	0.431	0.89	0.24	34.82	< 0.0001	48	46
Mesic, within subsystem	Functional group richness	Cover (log)	0.390	0.94	0.15	29.39	< 0.0001	48	46
Mesic, within subsystem	Effective functional group richness	Cover (log)	0.351	0.82	0.34	24.93	< 0.0001	48	46
Mesic, within subsystem	Total species per functional group	Residuals of Total functional group richness - Cover (log)	0.290	-0.296	0.17	18.77	< 0.0001	48	46
Mesic, within subsystem	Effective species per functional group	Residuals of Effective functional group richness - Cover (log)	0.204	-0.41	0.35	11.80	0.001	48	46
Mesic, within subsystem	Composition	Cover (log)	0.494			4.69	0.004	30	24

Table 1 continued. Summary statistics from linear regressions and ANOVAs for diversity, ecosystem function, and invasibility.

Understory plant diversity, composition, and decomposition

Subsystem, scale	Independent Variable (transformation)	Dependent Variable (transformation)	R^2	Inter-cept	Coeff.	F	*P*	N	df
All, across subsystems	Total species richness	Litter mass loss	0.000	13.03	-0.02	0.02	0.886	55	53
All, across subsystems	Cover (log)	Litter mass loss	0.000	13.06	-0.08	0.01	0.911	55	53
Seep, within subsystem	Total species richness	Litter mass loss	0.000	14.43	0.03	0.04	0.843	31	29
Seep, within subsystem	Effective species richness	Litter mass loss	0.000	14.66	0.00	0.00	0.993	31	29
Seep, within subsystem	Cover (log)	Litter mass loss	0.000	14.05	0.31	0.01	0.906	31	29
Seep, within subsystem	Functional group richness	Litter mass loss	0.002	14.27	0.08	0.05	0.828	31	29
Seep, within subsystem	Effective functional group richness	Litter mass loss	0.000	14.55	0.04	0.01	0.916	31	29
Seep, within subsystem	Composition	Litter mass loss	0.072			0.35	0.716	12	9
Mesic, within subsystem	Total species richness	Litter mass loss	0.110	11.41	0.38	5.54	0.023	47	45
Mesic, within subsystem	Effective species richness	Litter mass loss	0.157	11.02	1.21	8.40	0.006	47	45
Mesic, within subsystem	Cover (log)	Litter mass loss	0.091	9.33	2.70	4.53	0.039	47	45
Mesic, within subsystem	Functional group richness	Litter mass loss	0.111	11.01	0.68	5.59	0.022	47	45
Mesic, within subsystem	Effective functional group richness	Litter mass loss	0.080	11.18	1.33	3.93	0.054	47	45
Mesic, within subsystem	Composition	Litter mass loss	0.151			0.85	0.527	30	24

Understory plant diversity, productivity, and invasibility

Subsystem, scale	Independent Variable (transformation)	Dependent Variable (transformation)	R^2	Inter-cept	Coeff.	F	*P*	N	df
All, across subsystems	Total species richness	Exotic invasive cover (log)	0.259	-0.10	0.07	60.56	< 0.0001	175	173
All, across subsystems	Cover (log)	Exotic invasive cover (log)	0.305	-0.22	0.40	75.81	< 0.0001	175	173
Seep, within subsystem	Total species richness	Exotic invasive cover (log)	0.002	0.53	0.01	0.07	0.798	31	29
Seep, within subsystem	Effective species richness	Exotic invasive cover (log)	0.045	0.34	0.07	1.35	0.255	31	29
Seep, within subsystem	Cover (log)	Exotic invasive cover (log)	0.189	-2.51	1.56	6.77	0.014	31	29

Table 2. Environment, understory plant diversity, and understory subsystem function.

Subsystem, scale	Environmental Variable (transformation)	Community/Ecosystem Variable (transformation)	Pearson's *r*	*P*
All, across subsystems	Soil moisture	Total species richness	0.401	**< 0.0001**
All, across subsystems	Soil moisture	Cover (log)	0.332	**0.002**
All, across subsystems	Soil moisture	Litter mass loss	0.179	0.263
All, across subsystems	Soil moisture	Exotic invasive cover (log)	0.625	**< 0.0001**
All, across subsystems	% Canopy openness	Total species richness	-0.410	**< 0.0001**
All, across subsystems	% Canopy openness	Cover (log)	-0.481	**< 0.0001**
All, across subsystems	% Canopy openness	Litter mass loss	-0.140	0.222
All, across subsystems	% Canopy openness	Exotic invasive cover (log)	-0.270	**0.006**
All, across subsystems	Leaf area index	Total species richness	0.425	**< 0.0001**
All, across subsystems	Leaf area index	Cover (log)	0.391	**< 0.0001**
All, across subsystems	Leaf area index	Litter mass loss	0.088	0.444
All, across subsystems	Leaf area index	Exotic invasive cover (log)	0.308	**0.017**
Seep, within subsystem	Soil O horizon depth (log)	Total species richness	0.182	0.336
Seep, within subsystem	Soil O horizon depth (log)	Effective species richness	-0.015	0.939
Seep, within subsystem	Soil O horizon depth (log)	Cover (log)	0.214	0.257
Seep, within subsystem	Soil O horizon depth (log)	Litter mass loss	-0.021	0.911
Seep, within subsystem	Soil O horizon depth (log)	Exotic invasive cover (log)	-0.125	0.502
Seep, within subsystem	Soil A horizon depth (log)	Total species richness	0.178	0.348
Seep, within subsystem	Soil A horizon depth (log)	Effective species richness	0.147	0.439
Seep, within subsystem	Soil A horizon depth (log)	Cover (log)	0.152	0.424
Seep, within subsystem	Soil A horizon depth (log)	Litter mass loss	0.214	0.256
Seep, within subsystem	Soil A horizon depth (log)	Exotic invasive cover (log)	0.161	0.387
Seep, within subsystem	Soil moisture	Total species richness	-0.161	0.396
Seep, within subsystem	Soil moisture	Effective species richness	-0.041	0.830
Seep, within subsystem	Soil moisture	Cover (log)	0.045	0.814
Seep, within subsystem	Soil moisture	Litter mass loss	-0.289	0.121
Seep, within subsystem	Soil moisture	Exotic invasive cover (log)	0.373	**0.039**
Seep, within subsystem	% Canopy openness	Total species richness	-0.077	0.680
Seep, within subsystem	% Canopy openness	Effective species richness	-0.005	0.997
Seep, within subsystem	% Canopy openness	Cover (log)	0.119	0.525
Seep, within subsystem	% Canopy openness	Litter mass loss	0.110	0.557
Seep, within subsystem	% Canopy openness	Exotic invasive cover (log)	-0.021	0.911

Table 2 continued. Environment, understory plant diversity, and understory subsystem function.

Subsystem, scale	Environmental Variable (transformation)	Community/Ecosystem Variable (transformation)	Pearson's *r*	*P*
Seep, within subsystem	Leaf area index	Total species richness	0.347	0.060
Seep, within subsystem	Leaf area index	Effective species richness	0.283	0.130
Seep, within subsystem	Leaf area index	Cover (log)	0.110	0.562
Seep, within subsystem	Leaf area index	Litter mass loss	-0.142	0.455
Seep, within subsystem	Leaf area index	Exotic invasive cover (log)	0.180	0.334
Mesic, within subsystem	Soil O horizon depth (log)	Total species richness	-0.125	0.398
Mesic, within subsystem	Soil O horizon depth (log)	Effective species richness	0.080	0.588
Mesic, within subsystem	Soil O horizon depth (log)	Cover (log)	-0.019	0.899
Mesic, within subsystem	Soil O horizon depth (log)	Litter mass loss	0.187	0.208
Mesic, within subsystem	Soil A horizon depth (log)	Total species richness	0.227	0.121
Mesic, within subsystem	Soil A horizon depth (log)	Effective species richness	0.298	**0.040**
Mesic, within subsystem	Soil A horizon depth (log)	Cover (log)	0.039	0.793
Mesic, within subsystem	Soil A horizon depth (log)	Litter mass loss	0.176	0.236
Mesic, within subsystem	Soil moisture	Total species richness	0.057	0.700
Mesic, within subsystem	Soil moisture	Effective species richness	-0.079	0.595
Mesic, within subsystem	Soil moisture	Cover (log)	0.001	0.996
Mesic, within subsystem	Soil moisture	Litter mass loss	-0.043	0.775
Mesic, within subsystem	% Canopy openness	Total species richness	-0.077	0.680
Mesic, within subsystem	% Canopy openness	Effective species richness	-0.005	0.977
Mesic, within subsystem	% Canopy openness	Cover (log)	0.119	0.525
Mesic, within subsystem	% Canopy openness	Litter mass loss	0.110	0.557
Mesic, within subsystem	Leaf area index	Total species richness	0.099	0.503
Mesic, within subsystem	Leaf area index	Effective species richness	0.172	0.241
Mesic, within subsystem	Leaf area index	Cover (log)	0.096	0.516
Mesic, within subsystem	Leaf area index	Litter mass loss	0.025	0.866

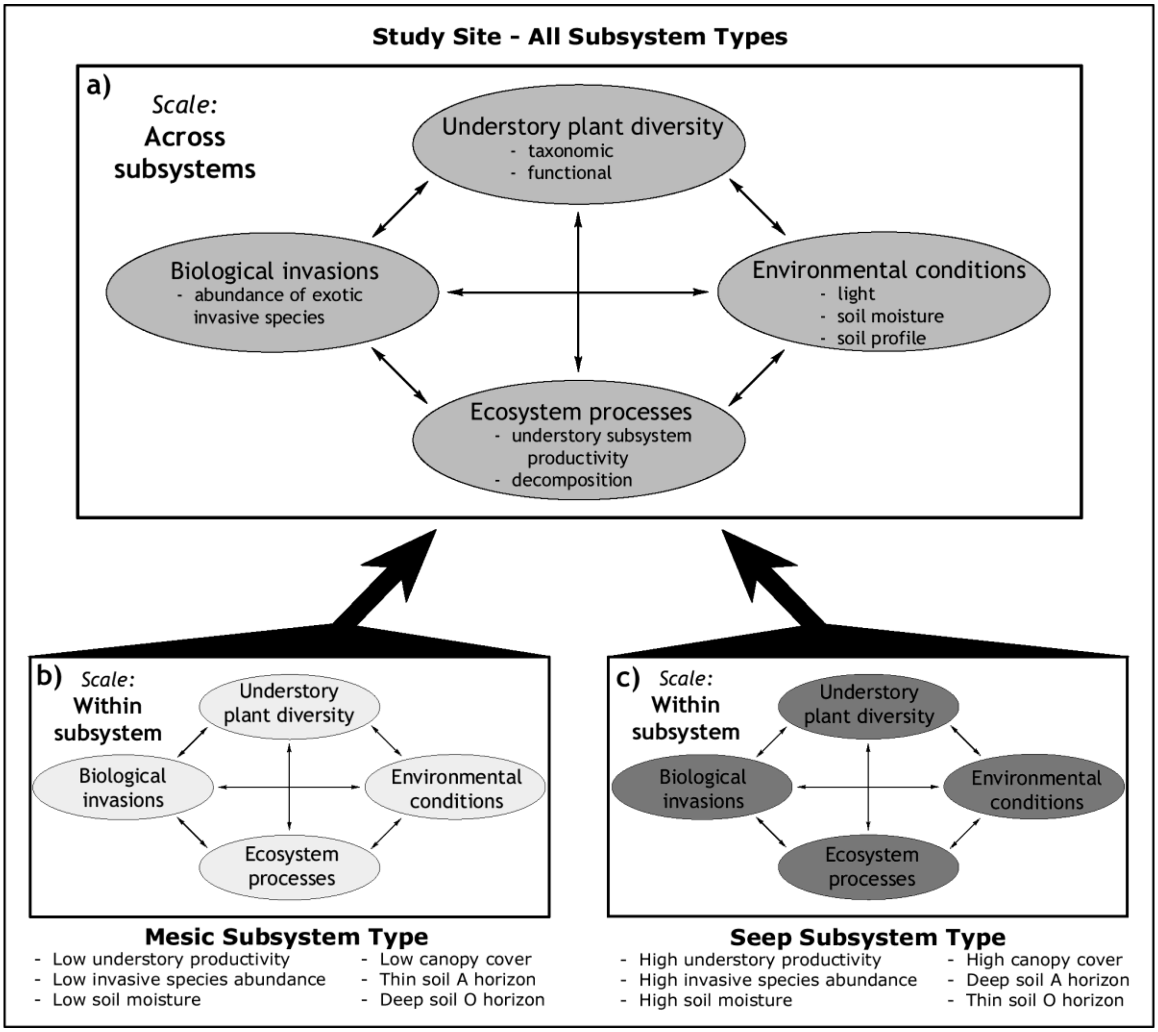


Figure 1. Study design for testing Biodiversity-Ecosystem Function-Invasibility (BEFI) relationships at two scales of ecological association a) across understory subsystem types, and b,c) within each of two subsystem types. For each component of scale, the same ecosystem interactions were studied. Arrows depict the interactions examined between understory plant diversity, biological invasions, environmental conditions, and ecosystem processes (measured variables are indicated below each). Mesic and seep subsystems differ dramatically in the indicated environmental, plant community, and ecosystem parameters. In the study site, mesic and seep areas are distributed in a mosaic with scattered seeps and an intervening mesic matrix, together forming the greater, across-subsystem scale of ecological association.

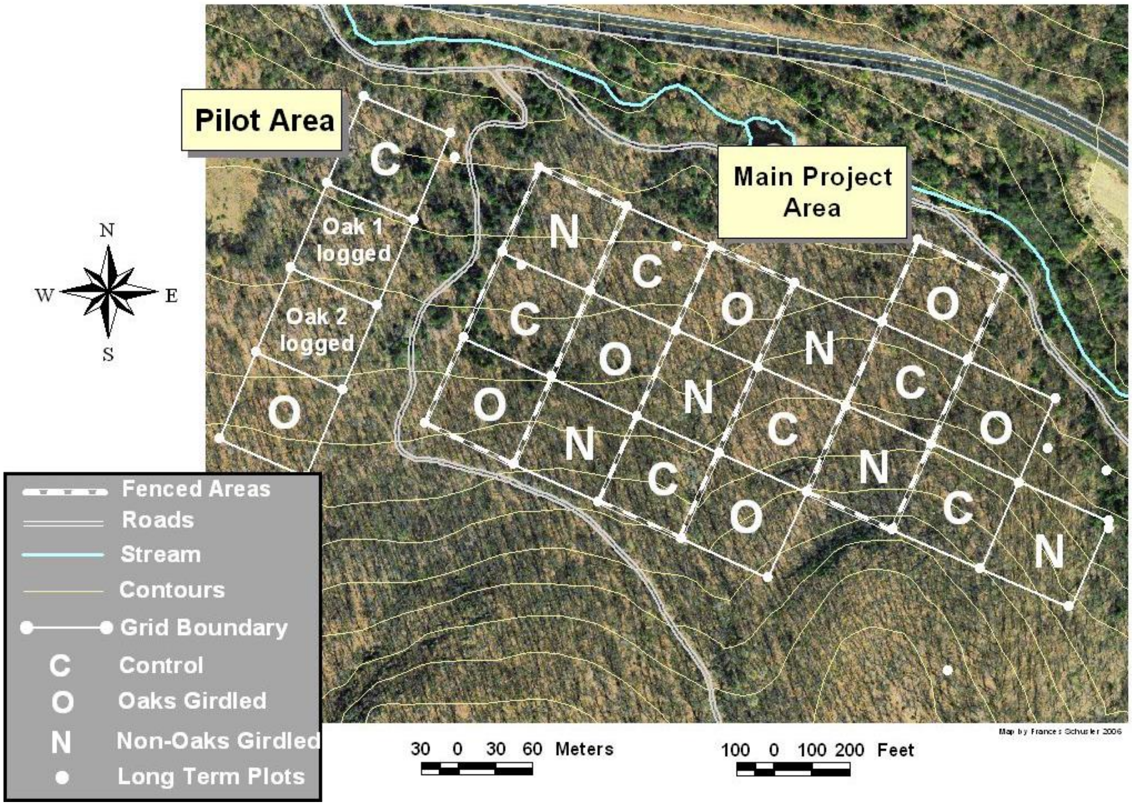


Figure 2. The study site at Black Rock Forest, Orange County, NY. Grid boundaries indicate the limits of twenty 5,625 m^2 plots, inside each of which the 625 m^2 plots are centered. Contours indicate 10 m increments in elevation, from 140 m at the base of the slope (top of photo). Letters indicate planned canopy removal treatments. Map courtesy of Frances Schuster, Black Rock Forest.

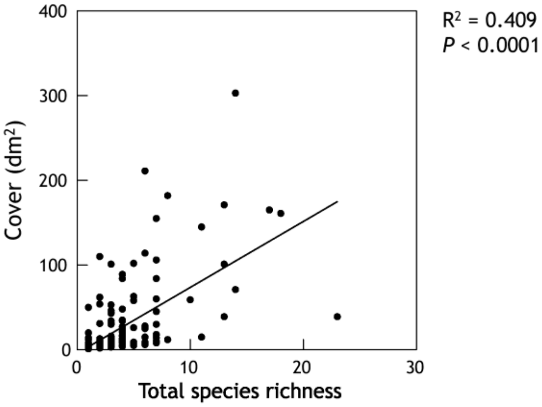
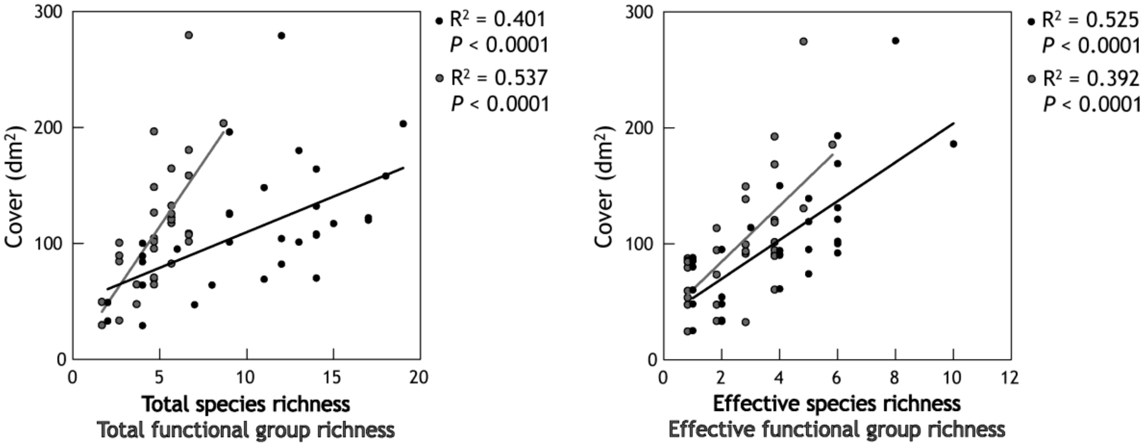


Figure 3. Total understory species richness correlated with cover across subsystems, *i.e.*, at the level of the study site.

Within Seep Understory Subsystem:



Within Mesic Understory Subsystem:

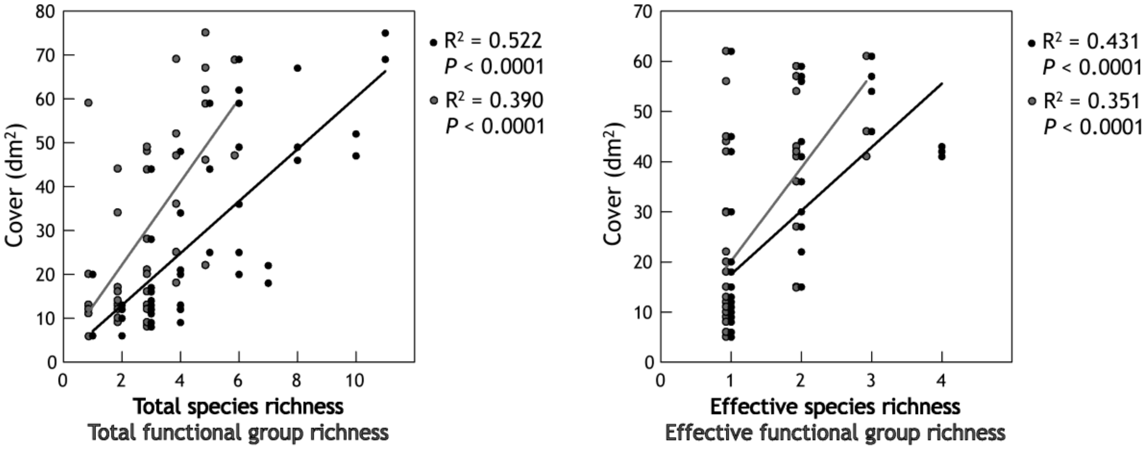


Figure 4. Understory plant taxonomic and functional group richness explained cover at within-subsystem scales. Black circles represent total and effective species richness, and open circles represent total and effective functional group richness.

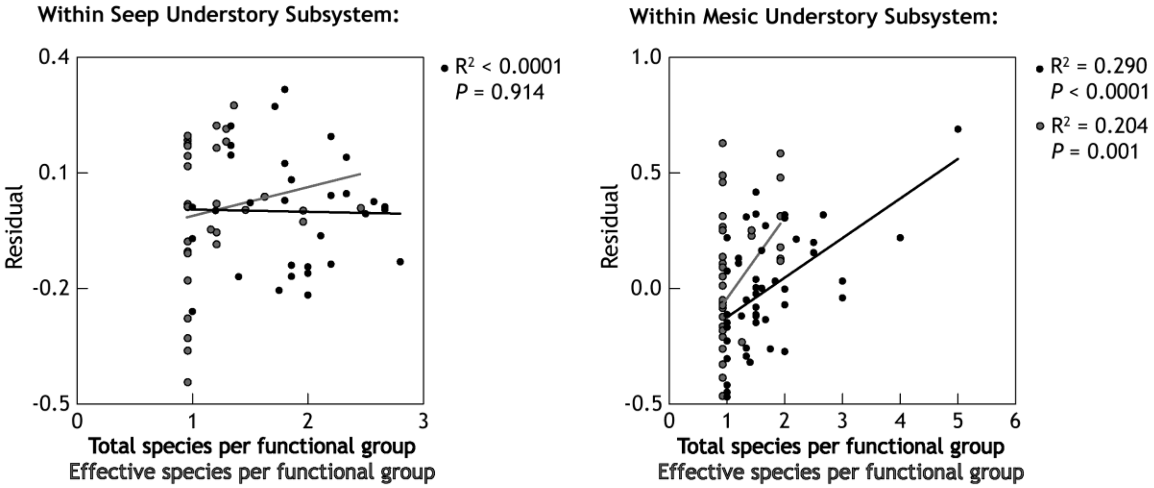


Figure 5. Within-functional group species richness of understory plants explained the residuals of linear regressions of cover on respective plant diversity metrics in the mesic subsystem, but not for total species per functional group in the seep subsystem. Black circles represent mean total species richness per functional group, and open circles represent mean effective species richness per effective functional group (high heteroschedasticity precluded regression of residuals on effective species per functional group).

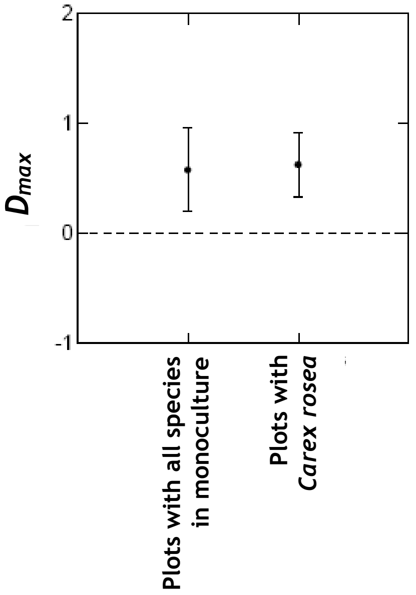


Figure 6. Transgressive overyielding (D_{max}) + 95% confidence intervals for polycultures in the mesic understory subsystem. Plots with all species in monoculture (N = 11) excludes all plots with *Carex rosea*, for which no monocultures could be located. In plots with *C. rosea* (N = 15), the monoculture value used for the cespitose sedge *C. rosea* was from *C. digitalis*, which had the highest monoculture value of all cespitose sedges.

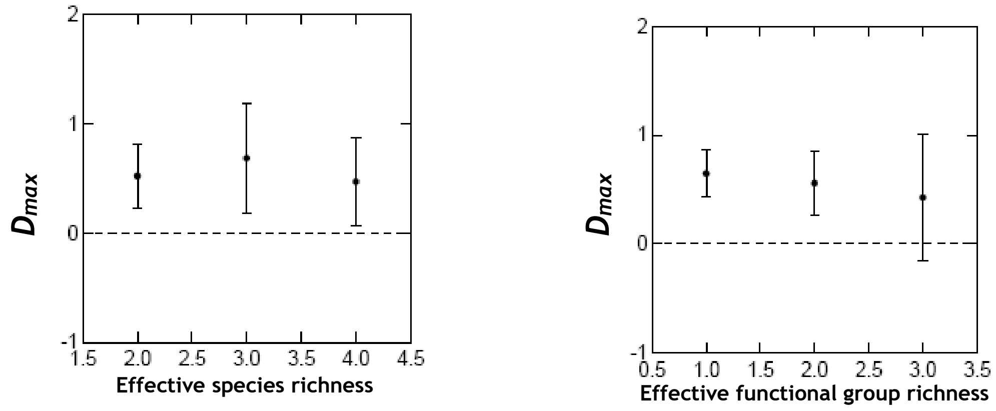


Figure 7. Transgressive overyielding (D_{max}) + 95% confidence intervals for all polycultures in the mesic understory subsystem, by effective species and functional group richness.

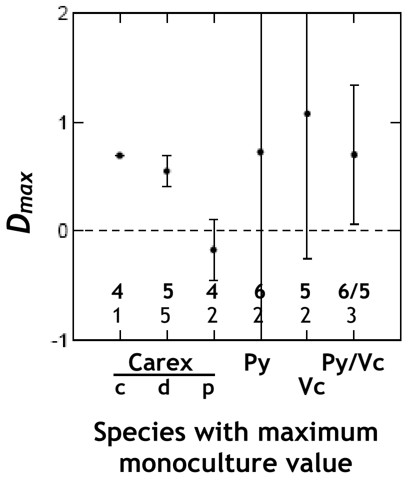


Figure 8. Transgressive overyielding (D_{max}) ± 95% confidence intervals for polycultures in the mesic understory subsystem, by species with the highest maximum monoculture value in a given plot (*i.e.*, the species most likely to prevent overyielding from occurring). Plain text values at the base of the figure indicate the number of polycultures for which the species had the maximum monoculture value, and boldface values indicate the number monocultures for the species. Plots including *C. rosea* are included under *C. digitalis.* Species codes are as follows: *Carex* c = *C. communis,* d = *C. digitalis,* p = *C. pensylvanica;* Py = *Polystichum acrostichoides;* Vc = *Vaccinium pallidum;* Py/Vc = *Polystichum acrostichoides* and *Vaccinium pallidum* both present (these species reached the same maximum monoculture value of 20 dm^2).

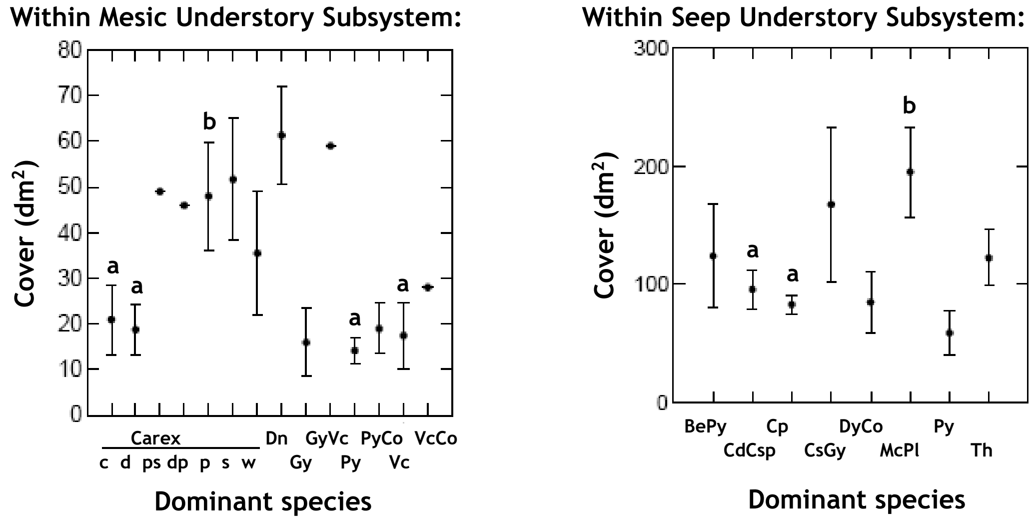


Figure 9. Cover (± SE) differed with composition of dominant understory plant species at within-subsystem scales. Letters indicate significant Least Significant Difference post-hoc tests for groups included in ANOVAs (Mesic subsystem: F = 4.69, *P* = 0.004; Seep subsystem: F = 10.36, *P* = 0.005). Species codes for the mesic subsystem are as in Figure 8, and as follows: *Carex* s = C. *stipata,* w = *C. swanii* (combinations of d, p, and s indicate co-dominance). Codes for the seep subsystem are as in Figure 8, and as follows: Dn = *Dennstaedtia punctilobula;* Gy = *Gaylussacia baccata*; Be = *Berberis thungbergii;* Cd = *Carex digitalis;* Csp = *Carex* spp.; Cp = *C. pensylvanica;* Cs = *C. stipata;* Dy = *Dryopteris* spp.; Mc = *Microstegium vimineum;* Pl = *Pilea pumila;* Th = *Thelypteris noveboracensis* (combinations of codes indicate co-dominance; Co = first species is co-dominant with 1+ other species).

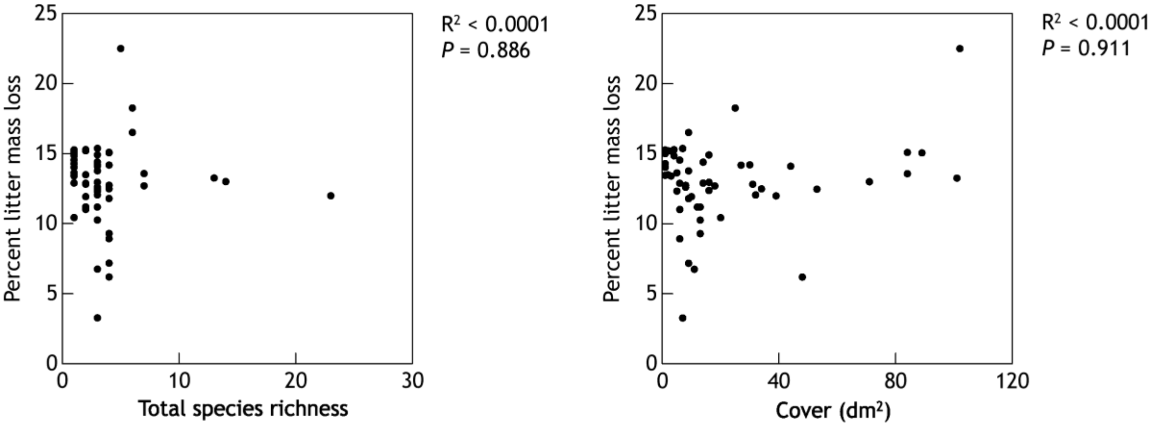


Figure 10. Percent litter mass loss showed no trends with total understory plant species richness or cover at the across-subsystem scale.

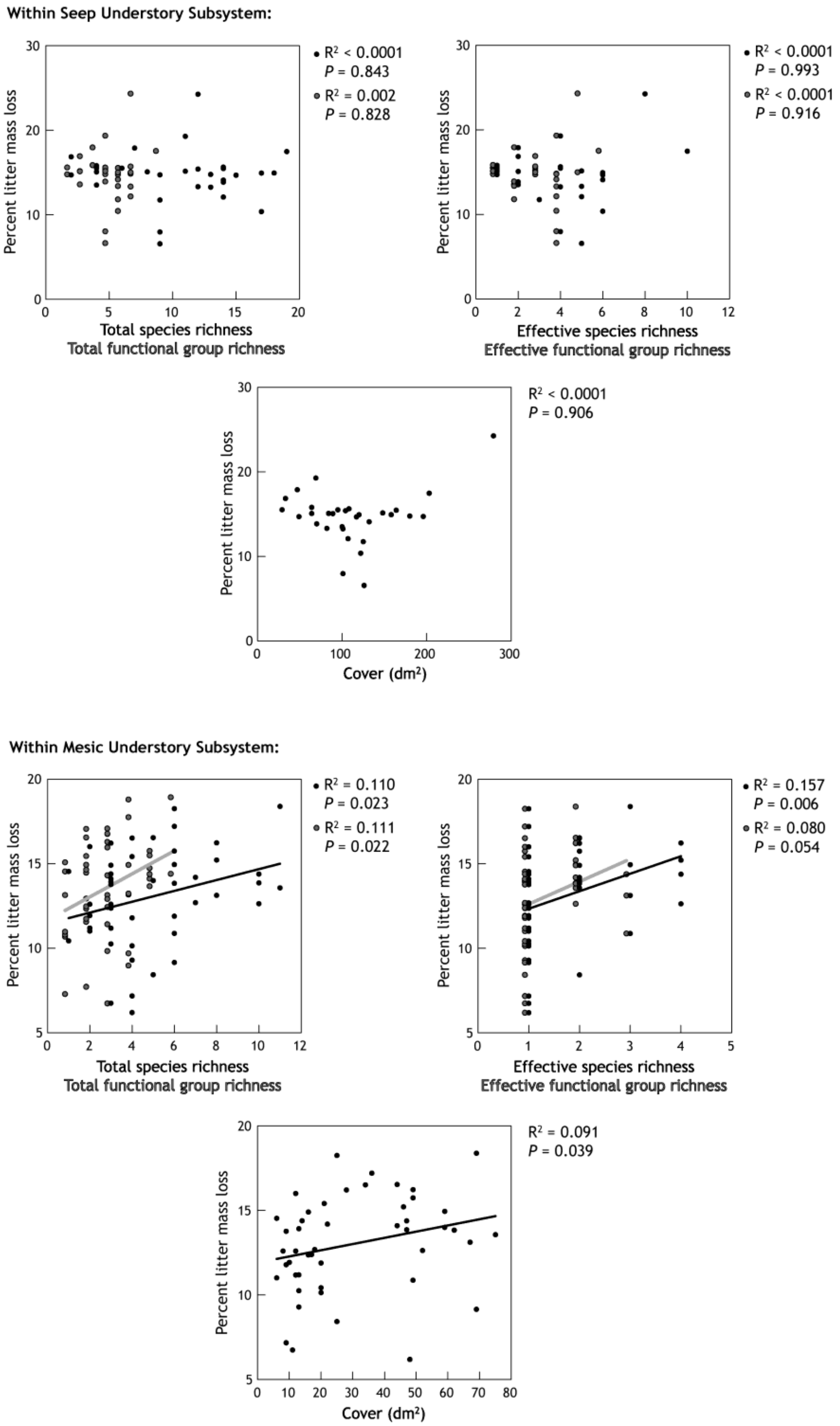


Figure 11. Total and effective understory plant species and functional group richness and cover explained percent litter mass loss within the mesic, but not seep, subsystems. Black circles represent total and effective species richness or cover, and open circles represent total and effective functional group richness.

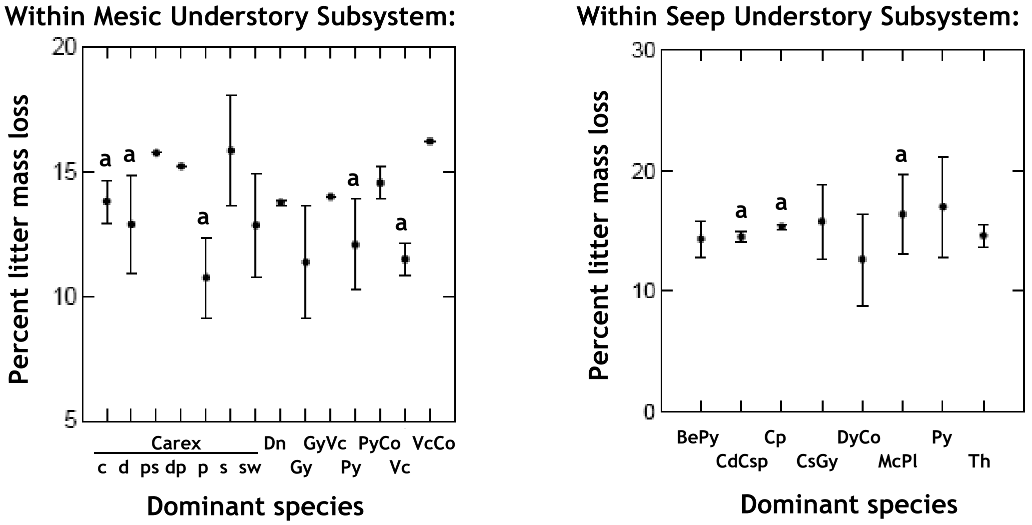


Figure 12. Composition of dominant understory plant species did not explain percent litter mass loss (± SE) at within-subsystem scales (Mesic subsystem: F = 0.85, *P* = 0.527; Seep subsystem: F = 0.35, *P* = 0.716). Letters indicate groups included in ANOVAs. Species codes are as in Figures 8 and 9.

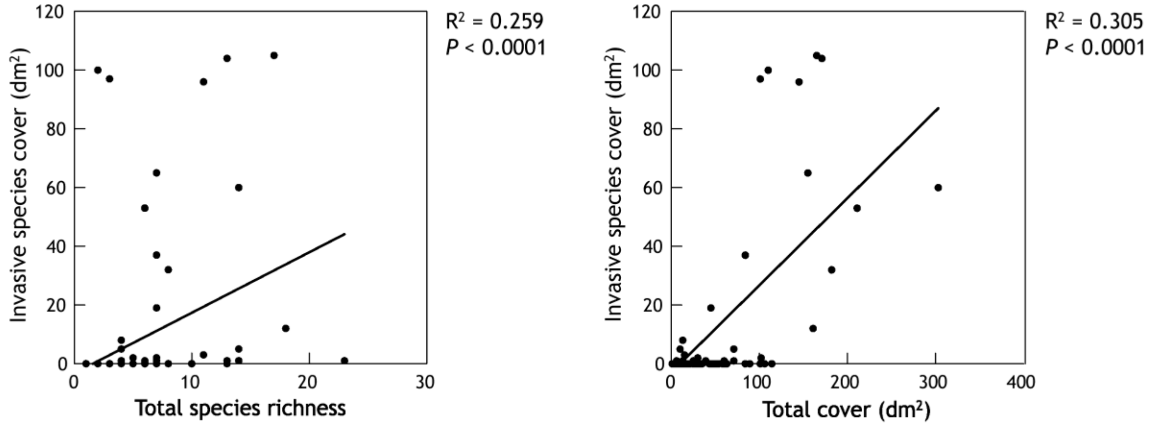


Figure 13. Invasibility correlated with total understory plant species richness and cover at the across-subsystem scale.

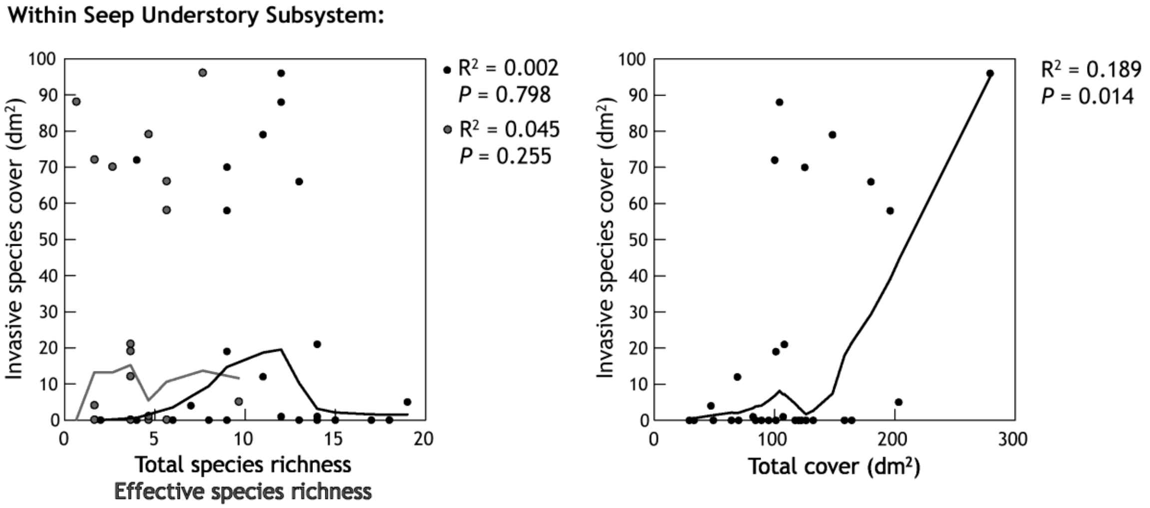


Figure 14. Invasibility correlated with cover, but not total or effective understory plant species richness, at the within-subsystem scale in seeps. Black circles represent total species richness or cover, and open circles represent effective species richness. Data are fitted with LOWESS functions with tension = 0.5.