Journal of Vegetation Science **23** (2012) 906–918

Scale-dependent responses of species richness to experimental manipulation of productivity and disturbance in Californian coastal grasslands

Brody Sandel & Jeffrey D. Corbin

Keywords
Experiments; Occurrence probabilities; Spatial scale; Species aggregation; Species–area relationships; α-diversity; β-diversity

Abbreviations
SAR = Species–area relationship; COP = Conditional occurrence probability; CEI = Community evenness index.

Nomenclature
Hickman (1993);

Received 22 November 2010
Accepted 11 February 2012
Co-ordinating Editor: Michael Huston

Sandel, B. (corresponding author, brody.sandel@biology.au.dk): Department of Integrative Biology, University of California, Berkeley, CA, 94720, USA
Corbin, J.D. (corbinj@union.edu): Department of Biological Sciences, Union College, Schenectady, NY, 12308, USA

Abstract

Question: Relationships between species richness and environmental drivers such as productivity and disturbance are sensitive to the scale over which they are measured, but the extent to which this scale-dependence is important for experimental studies conducted over small scale ranges is not well known. We ask whether the response of species richness to experimental manipulation of productivity and disturbance varies across small spatial scales (0.016–4 m^2). We show that species–area relationships are well suited to summarize cross-scale responses of species richness, and ask whether the responses of species–area relationships to experimental manipulations are more consistent than richness at any single scale.

Location: Northern Californian coastal grasslands.

Methods: We applied disturbance and productivity reduction treatments over 4 yr at two sites. We assessed changes in species richness over five grain sizes, encompassing a 256-fold range of plot size. This allowed us to construct a species–area relationship for each experimental plot in each sampling year. We used the slope of the species–area relationship to summarize changes in species richness across multiple spatial scales.

Results: Richness responses were scale-dependent and complex, causing changes at any one scale to be difficult to interpret. Disturbance either increased or had no effect on richness, while reducing productivity had idiosyncratic effects among sites, scales and years. Both treatments, however, had consistent and interpretable effects on the species–area relationship. Reducing productivity increased the slope of the species–area relationship, while disturbance decreased it.

Conclusions: Our results suggest that the productivity–richness and disturbance–richness relationships are scale-dependent, and that improved generality could be achieved by focusing attention on the response of the species–area relationship to these factors.

Introduction

Understanding the causes of variation in species richness is one of the central enterprises of community ecology. It is becoming increasingly clear that progress in this area will depend heavily on understanding how spatial scale influences richness patterns (Wiens 1989; Levin 1992; Mittelbach et al. 2001; Whittaker et al. 2001; Sandel & Smith 2009). Different factors are important in determining species richness at different spatial scales (Ricklefs 1987; Huston 1999; Willis & Whittaker 2002), while particular factors can have different effects depending on scale (e.g. Olff & Ritchie 1998). These challenges are well known in ecology, but relatively few studies have grappled with them directly by examining patterns across multiple spatial scales (Hewitt et al. 2007; Ellis & Schneider 2008; Sandel & Smith 2009). Experimental treatment effects, in particular, are rarely examined at multiple spatial scales.

This is a significant missed opportunity, as multi-scale sampling (1) improves detection of subtle treatment

Doi: 10.1111/j.1654-1103.2012.01406.x

effects, (2) bridges gaps between studies, possibly explaining discrepancies between them, and (3) improves mechanistic interpretations of treatment effects (Sandel & Smith 2009). However, the extra effort required to perform sampling at multiple scales is only worthwhile if results are likely to be scale-dependent over the range of scales considered. Here, we ask if scale-dependent changes in species richness, which are well known over large spatial scales, are also important to consider over scale ranges commonly used in manipulative experiments.

If scale-dependent responses of richness to experimental treatments prove common, this will have profound implications for our interpretation of experimental results. First, experiments that found no response to a treatment might have simply been looking at the wrong scale; effects might have been present if measured at a different scale (Kaiser 2003; Dumbrell et al. 2008). On the other hand, positive results must also be viewed with caution if extrapolating to other scales, because effects present at the sampled scale might not persist at larger or smaller scales (Levine & D’Antonio 1999; Chesson et al. 2005). Scale-dependence also provides a potential general explanation for mismatches among experimental results and between experiments and observational studies, so that considering it explicitly may yield improved generalization regarding the factors that control species richness (Sandel & Smith 2009).

Species–area relationships

Species–area relationships (SARs) are particularly useful tools to understand richness responses across multiple spatial scales. Their use does not require the arbitrary distinction of within- (α) and between-plot (β) components of diversity because scale is instead treated as a continuous variable. In addition, the theoretical underpinnings of SARs are well understood, allowing sophisticated interpretations of SAR changes with experimental treatments (e.g. He & Legendre 2002; Tjørve et al. 2008). Treating the SAR, rather than a richness measure at a single scale, as the response variable in ecological experiments has interesting consequences. First, it admits the possibility that treatment effects on richness may be more complex than simply ‘it increases’ or ‘it decreases’. A particular treatment may increase species richness at one spatial scale but decrease it at another, if the control and treatment SARs cross. This produces a treatment effect that is qualitatively scale-dependent. More subtly, the magnitude, but not the direction, of a treatment effect may change as a function of scale, producing quantitative scale dependence. Clearly, under these circumstances single-scale studies have the potential to produce conflicting results, and can provide an oversimplified or misleading assessment of treatment effects (Sandel & Smith 2009). Thus, examining richness responses across multiple scales allows a more precise understanding of treatment effects.

Changes in the SAR within a plot must be caused by some combination of changing overall richness, the abundance distribution of species or the degree of spatial aggregation of species distributions (He & Legendre 2002; Harte et al. 2008; Tjørve et al. 2008). To illustrate this, consider the effect of adding one species to a plot. Clearly, this raises at least the right-hand portion of the SAR within that plot. The extent to which this increase is seen throughout the SAR depends on the abundance of the added species and on the spatial pattern of its distribution (He & Legendre 2002). Abundant and evenly distributed species will tend to influence the left-hand portion more strongly than rare or patchily distributed species. Experimental manipulations can alter both the abundance and aggregation of species within a community, leading to potentially complex responses of the SAR to experimental treatments. These components can be useful, for example, in understanding human impacts on reef fish assemblages (Tittensor et al. 2007).

Productivity and disturbance

Two well-studied factors that are known to have important and scale-dependent effects on species richness are productivity and disturbance. In both cases, an array of experimental and observational studies from a wide range of spatial scales has yielded a set of conflicting results. Experiments are useful tools to uncover the relationship of productivity and disturbance with species richness, but few experimental studies to date have examined the response of species richness across multiple spatial scales (but see Allcock & Hik 2003; Crawley et al. 2005; de Bello et al. 2007).

The relationship between species richness and productivity is generally positive at large spatial scales (Reichle 1970; Francis & Currie 2003; Hawkins et al. 2003), but may be unimodal or negative at smaller spatial scales (e.g. Grime 1973, 1979; Al-Mufti et al. 1977; Silvertown 1980; Aerts & Berendse 1988; Tilman 1993; Mittelbach et al. 2001). Small-scale experimental fertilization studies typically find a decrease in richness with increased productivity (Gough et al. 2000). The degree to which this mismatch is due to differences in sampling scale as opposed to experimental artifacts is unclear, but these conflicting results certainly suggest that different processes appear to be important at different spatial scales (Mittelbach et al. 2001; Chase & Leibold 2002; Chalcraft et al. 2004; Harrison et al. 2006). One explanation for this is the decoupled responses of α (within-plot) and β (between-plot) components of diversity to productivity (Chase & Leibold 2002).

Increasing productivity might decrease α-diversity but increase β-diversity, leading to scale-dependent changes in richness. Indeed, a meta-analysis of experimental results revealed that, while increasing productivity leads to a decrease in α-diversity, it can also lead to an increase in β-diversity, particularly at low-productivity sites (Chalcraft et al. 2008).

Community responses to disturbance can also be scale-dependent. Species richness at any particular spatial scale may be maximized under intermediate disturbance intensity and frequency (e.g. Loucks 1970; Connell 1978; Huston 1979; Sousa 1979), but a major disturbance at one spatial scale can be a minor disturbance at a larger scale. This can cause empirical disturbance–richness relationships to vary as a function of spatial scale, resulting in conflicting conclusions that resist generalization, particularly when scale is not considered explicitly (Hamer & Hill 2000; Mackey & Currie 2001; Kaiser 2003; Tylianakis et al. 2006). Multi-scale studies of tropical lepidopterans have shown that their response to disturbance varies with the spatial scale of sampling, typically increasing with disturbance at small scales and decreasing at larger scales (Hamer & Hill 2000; Dumbrell et al. 2008). This suggests that the general pattern of richness responses to increasing disturbance may be a decrease in the slope of the SAR. Disturbance–richness relationships at any particular single scale may be idiosyncratic and determined in large part by the relatively arbitrary choice of sampling scale.

In this paper, we ask whether the response of vascular plant species richness to experimental manipulations of productivity and disturbance are scale-dependent. We use SARs to summarize treatment effects, and examine causes of changes in the SAR over 4 yr and at two coastal grassland sites in California. In so doing, we demonstrate the above three benefits of multi-scale sampling in ecological experiments.

Methods

Study sites

This study was conducted in two coastal grasslands in western Marin County, California: Tom's Point and Point Reyes. Tom's Point (38°13′N, 122 57′W) is a private reserve owned by Audubon Canyon Ranch. The Point Reyes site is located at Pierce Point Ranch, in the Point Reyes National Seashore (38°11′N, 122°57′W). Both sites are dominated by exotic grasses, including *Bromus diandrus* Roth, *Vulpia myuros* L., *Holcus lanatus* L. and *Lolium perenne* L. Native species are rare at both sites, and include *Bromus carinatus* Hook & Arn., *Elymus glaucus* Buckley, *Eschscholzia californica* Cham. and, to a lesser extent, *Hordeum brachyantherum* Nevski and *Danthonia californica* Bol. Both sites have been free from livestock grazing for at least 35 yr, though the Point Reyes site is visited frequently by native Tule elk (*Cervus elaphus nannodes*). The sites typically receive between 60 and 100 cm of precipitation each growing season, concentrated from October until April. The winter of 2005–2006 was unusually wet, with approximately 120 cm of rain, while rainfall in the remaining years of this study ranged between 50 and 65 cm per growing season (PRISM Climate Group, Oregon State University 2010).

Treatments

In October 2005, we established 48 plots at each of the two sites. These plots were arranged to avoid areas dominated by *Lupinus arboreus* Sims and *Baccharis pilularis* DC. shrubs, which are abundant at both sites. Plots were 5 m × 5 m at Point Reyes and, due to space limitations, 4 m × 4 m at Tom's Point.

Plots were randomly assigned to one of three treatments: reverse fertilization, disturbance and control. Reverse fertilization was accomplished by adding a carbon source to the soil twice each year. Soil microbial populations increase in response to this increase in C availability. As they do, soil N becomes immobilized in microbial biomass, making it temporarily unavailable to plants (Schlesinger 1997). Carbon was added in the spring and autumn of each year at a rate of 450 g·sucrose·m^{-2}, except the initial treatment, which was 170 g·sucrose·m^{-2} and 360 g·sawdust·m^{-2}. Our disturbance treatment was a mid-season mowing. Mowing occurred in late March or early April of 2006, 2007, 2008 and 2009, and reduced the height of vegetation to ca. 10 cm. Following mowing, we removed all clippings from the plots. Half of the plots also received a mix of native grass seed each autumn, but native establishment was extremely rare, and we ignore that treatment here.

Sampling

At the end of the growing seasons of 2006, 2008 and 2009, we clipped all standing biomass from subplots within treatment plots. In July 2006, we sampled biomass from two 50 cm × 50 cm squares in half of the treatment plots at each site (n = 8), while in 2008 and 2009 we collected biomass samples from two 25 cm × 25 cm squares from all experimental plots. These samples were dried and weighed.

We surveyed the plant assemblage in each plot at the beginning of the summer (primarily June) of 2006, 2007, 2008 and 2009. The sampling unit was a 2 m × 2-m plot arrayed in the middle of each treatment plot. This unit was gridded into 16 50 cm × 50 cm cells, each of which contained a 25 cm × 25-cm subplot, which in turn contained a 12.5 cm × 12.5-cm subplot. During each sampling year,

Doi: 10.1111/j.1654-1103.2012.01406.x

we identified all vascular plant species rooted in each cell and subplot. This design allowed us to assess the presence or absence of all vascular plant species at five spatial scales, each a factor of four larger than the last. The range of plot sizes examined in this study is 0.016–4 m^2.

Analysis

We summarized the spatial pattern of species richness for each plot by calculating the slope of the SAR for that plot. Slopes were calculated by taking the mean species richness at each scale (within each plot, n = 16, 16, 16, 4 and 1 for the five grain sizes), and regressing log (mean richness) against log (area). Additionally, we described the intercept of the SAR using the average richness of the smallest subplots. We tested for treatment effects using repeated-measures ANOVAs, with treatment and site as fixed effects, and plot SAR slopes or smallest-scale richness measured repeatedly across multiple years.

This approach has the advantage of directly describing the characteristics of the SAR, but ignores within-plot variation and uncertainty in the estimate of the SAR slope and smallest-scale richness. We also investigated an alternative testing approach, using a linear mixed effects model to test for variation in subplot species richness as a function of treatment, site and spatial scale and their interactions (fixed effects) and plots nested within years (random effects). A scale-dependent treatment effect would be evidenced by a treatment × scale interaction.

The degree of aggregation of a species' spatial distribution can be summarized by calculating the conditional probability that it occurs in an area A, given that it occurs in a larger area B that includes A (Harte et al. 2005). We call this the conditional occurrence probability (COP) for a species. This approach to measuring spatial aggregations is related to methods used in macroecology (e.g. the P–area relationship and fractal dimensions, Šizling & Storch 2004; Storch et al. 2008); similar approaches have also seen some use in small-scale descriptions of species distributions and SARs (e.g. fractal community structure, Bossuyt & Hermy 2004). Conditional occurrence probabilities will be high for species with even spatial distributions and low for species with highly aggregated distributions. However, these probabilities are also strongly controlled by a species' abundance, as common species will tend to occupy an area B more completely than would a rare species (Harte et al. 2005).

We wanted to separate the roles of abundance changes and changes in spatial aggregation, so we calculated treatment-induced changes in COPs while introducing a novel method to control for differences in species abundances. Our method involves comparing the observed COP across all species within a plot to the expected values, given those species abundances and tendencies to aggregate. For each subplot of a particular size within each plot, we first determined the proportion of species that occurred at that scale that also occur at the next smaller scale. For example, if six species occurred within a particular 50 cm × 50 cm subplot and four of those species also occurred within a 25 cm × 25 cm section of that subplot, the community-wide COP for that subplot would be 0.667.

To take into account variation among species (as particular species vary in abundance and tendency to aggregate), we calculated the mean COP for a specific pair of spatial scales for each species for each combination of site and year. These mean values allowed us to predict, for any particular assemblage of species within a subplot, the expected community-wide COP, by simply averaging across the COP values for all species present. If species within a subplot are unusually even (relative to what one would expect given each species' abundance and propensity for aggregation), the observed community-wide COP value of a plot will exceed the expectation. Finally, for each subplot, we calculated a community evenness index (CEI), a new index that we defined as the mean difference between observed and expected community-wide COPs across all subplots within a plot. A CEI greater than zero indicates unusual evenness, while a value less than zero indicates spatial clumping. We calculated separate CEI values for all plots based on COPs between the 0.25 and 0.063 m^2 scales, and between the 0.063 and 0.016 m^2 scales.

We then asked whether a species' natural abundance at a site (estimated using its control plot occupancy rate) predicts its response to these treatments. We divided species into two classes – common and rare – based on their rate of occupancy in control plots. Species that occurred in at least 20% of the 50 cm × 50 cm sampling cells in control plots in a particular site and year were classified as common for that site and year, while all species present at lower abundances were classified as rare. Though somewhat arbitrary, our results were not sensitive to this 20% cut-off. For each species occurring in each site and year, we then calculated a treatment effect size on its occurrence rate, as the occurrence rate in treatment plots minus the occurrence rate in control plots. We performed an ANOVA with species rarity, site and year as fixed factors and the treatment effect size as the response variable. Because the treatment effect size is calculated separately for disturbance and reverse fertilization treatments, we performed a separate ANOVA for each of these two treatments.

Results

Both mowing and reverse fertilization reduced end-of-season above-ground biomass (Table 1). These changes were associated with large decreases in N availability and

Table 1. Above-ground biomass (g m^{-2}) in each treatment, site and year. Values are means (and standard errors).

Site	Treatment	2006	2008	2009
Point reyes	Control	617 (26)	571 (42)	202 (27)
	Rev. Fert.	497 (59)	385 (23)	157 (13)
	Disturb.	380 (18)	480 (29)	150 (12)
Tom's point	Control	583 (27)	765 (58)	244 (16)
	Rev. Fert.	478 (74)	539 (42)	209 (22)
	Disturb.	497 (29)	442 (20)	233 (22)

increased bare ground with reverse fertilization (Sandel et al. 2011). Reverse fertilization and mowing reduced above-ground biomass to similar extents in many cases. While particular species responded strongly to the treatments, such as the native N-fixing *Lupinus bicolor* Lindl. (increased with reverse fertilization) and the exotic forb *Rumex acetosella* L. (increased with mowing), functional groups were a poor predictor of species responses. Reverse fertilization plots, however, were characterized by a predominance of large-seeded and short species, while mowed plots were characterized by short species with high specific leaf area. Additional details on ecosystem- and community-level treatment responses can be found in Sandel et al. (2011).

Species–area relationships were well fitted by a power law relationship (average $r^2 = 0.979$), with a mean slope (z-value) of 0.259. This closely matches other small-scale SARs (Rosenzweig 1995; Drakare et al. 2006). Despite generally high r^2 values, most SAR slopes decreased slightly with increasing spatial scale, as is commonly found for SARs in this scale range (see Figs S1 and S2 in Supporting Information; Rosenzweig 1995; Carey et al. 2006). This pattern is expected when a community contains a large number of species with moderate occupancy (Tjørve et al. 2008), and has also been found to be associated with early-successional communities (Carey et al. 2006).

In some cases, the average SAR for treatment plots crossed that for control plots (Figs 1 and 2). In these cases, the effect of reverse fertilization and disturbance depended qualitatively on spatial scale. The slope of the SAR responded strongly to the treatments (Table 2, Fig. 3a,b). At both sites, reverse fertilization increased SAR slope relative to the control. Disturbance tended to reduce slopes

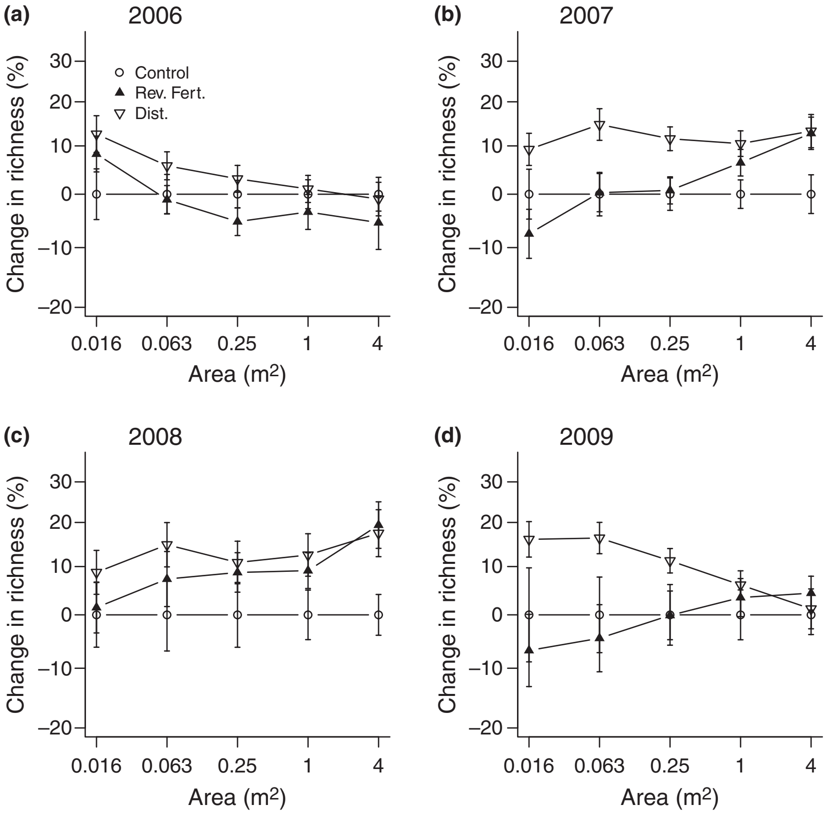

Fig. 1. Species–area relationships at Point Reyes, standardized to the control mean at each plot size. Standardization was performed by subtracting the control mean richness from each plot for each scale site and year (means were ln-transformed prior to standardization). Disturbance increased richness relative to the control, at all scales (2007 and 2008), or only at small scales (2009). Reverse fertilization typically had no or negative effects on richness at small scales, but positive effects at larger scales. Error bars are the standard error of richness values across 16 plots.

Doi: 10.1111/j.1654-1103.2012.01406.x

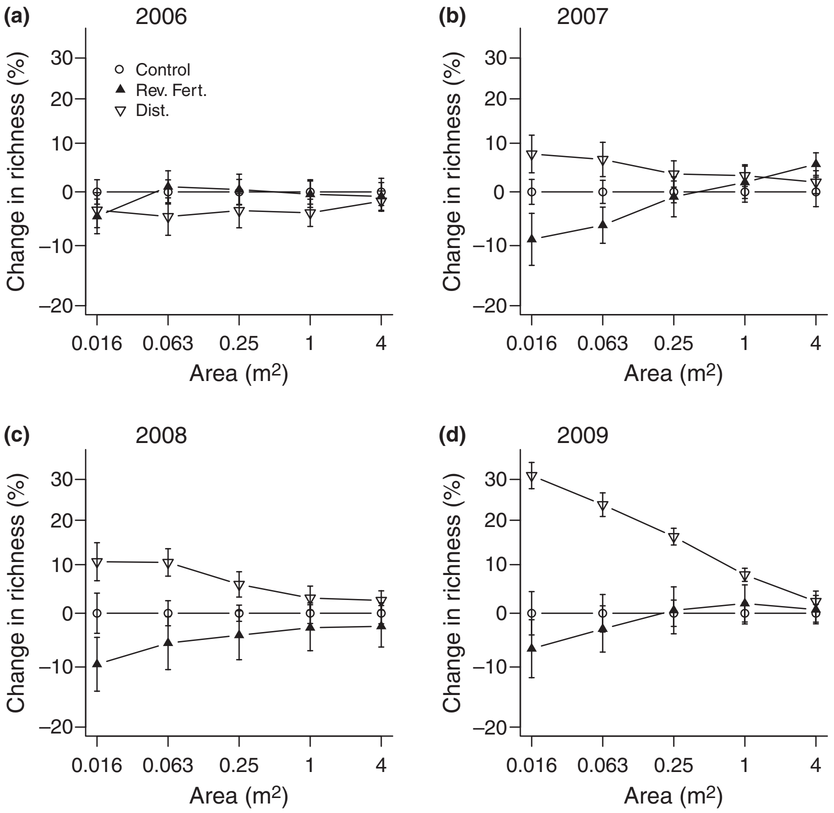

Fig. 2. Species–area relationships at Tom's Point, standardized to the control mean at each plot size (see Fig. 1). Disturbance typically increased richness, but only at small spatial scales. Reverse fertilization reduced richness at small scales, but had no or slightly positive effects at larger scales. Error bars are the standard error of richness values across 16 plots.

Table 2. ANOVA table for repeated measures ANOVA, testing the effect of treatment on species–area relationship slope.

	df	MSE	*F*	*P*
Site (*S*)	1	0.1417	56.96	<0.00001
Treatment (*T*)	2	0.0248	9.982	0.00012
S × *T*	2	0.0007	0.295	0.74
Residuals	90	00.25		
Year (*Y*)	3	0.0668	87.94	<0.00001
S × *Y*	3	0.0056	7.389	0.00008
Y × *T*	6	0.0054	7.084	<0.00001
S × *Y* × *T*	6	0.0012	1.518	0.17
Residuals	270	0.0007		

relative to the control, especially at Tom's Point. Hence, the magnitude of the treatment effect on richness also generally depended on scale. Mowing consistently increased smallest-scale richness (more elevated SARs), while reverse fertilization tended to slightly reduce smallest-scale richness, particularly at Tom's Point (Table 3, Fig. 3c,d).

The mixed effects linear models considering each individual estimate of richness within each plot, year and scale confirmed these basic results. The treatments had no significant main effects ($|t_{90}| < 0.85$, $P > 0.4$), but did show significant interactions with sampling scales ($|t_{19732}| > 2.8$, $P < 0.005$), reflecting the change in SAR slopes induced by the treatments. Interactions between site and treatment were not significant ($|t_{19732}| < 0.8$, $P > 0.4$).

Species that were common in control plots tended to be less frequent in reverse fertilization plots, while uncommon species became more frequent ($F_{1,282} = 24.18$, $P < 0.0001$; Fig. 4a,b). In contrast, disturbance differentially benefited common species, with no effect on rare species ($F_{1,280} = 11.01$, $P = 0.0010$; Fig. 4c,d).

Considering the CEI based on occurrence probabilities at 0.063 m^2, conditional upon occurrence at 0.25 m^2, disturbance tended to increase evenness of species distributions, leading to more homogenous plots ($F_{2,90} = 7.042$, $P = 0.0014$), although responses varied among years (Treatment × Year interaction $F_{6,270} = 2.737$, $P = 0.0134$; Fig. 5c,d). There were also effects in some years of reverse fertilization, towards more aggregated distributions, particularly at Tom's Point. Considering the CEI based on 0.016 m^2 occurrence probabilities, conditional on 0.063 m^2 occurrence probabilities, disturbance caused weak shifts towards increased evenness, while reverse

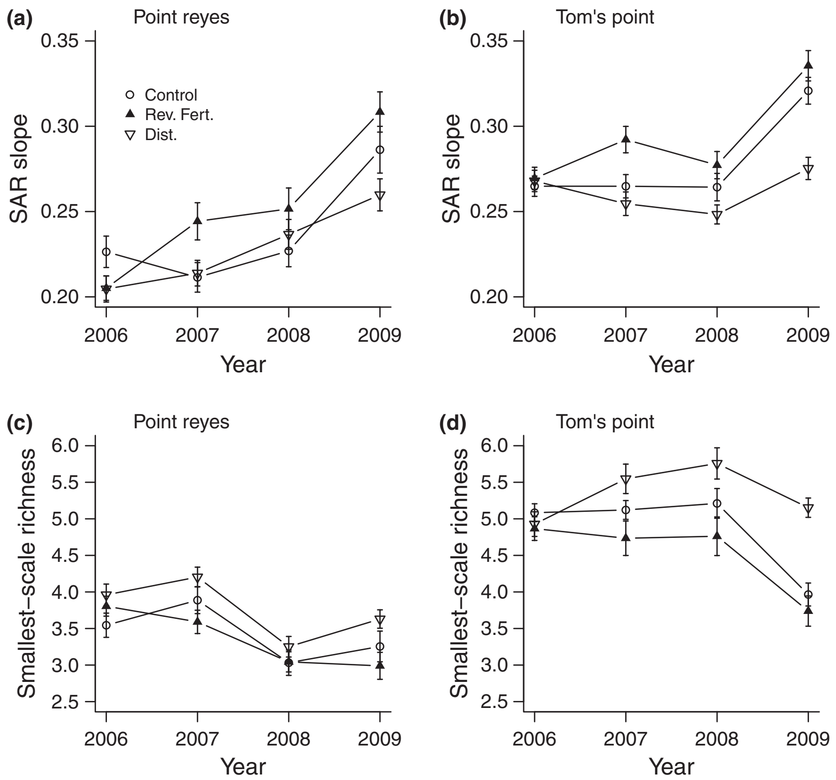

Fig. 3. Responses of species–area relationship (SAR) slopes (a,b) and smallest-scale richness (c,d) to experimental treatments. At both Tom's Point and Point Reyes, reverse fertilization increased the SAR slope in the last 3 yr of the study, while mowing decreased it, most strongly at Tom's Point. Mowing typically increased smallest-scale richness, while reverse fertilization slightly reduced it. Error bars represent standard errors of SAR slopes.

Table 3. ANOVA table for repeated measures ANOVA, testing the effect of treatment on smallest-scale richness.

	df	MSE	*F*	*P*
Site (*S*)	1	185.5	167.2	<0.00001
Treatment (*T*)	2	12.52	11.28	0.00004
S × *T*	2	1.408	1.269	0.29
Residuals	90	1.110		
Year (*Y*)	3	9.454	33.70	<0.00001
S × *Y*	3	6.193	22.07	<0.00001
Y × *T*	6	1.292	4.605	0.00018
S × *Y* × *T*	6	0.787	2.805	0.0115
Residuals	270	0.2805		

fertilization increased aggregation ($F_{2,90} = 3.636$, $P = 0.0303$; Fig. 5b,c).

Discussion

Scale dependence and experiments

Scale dependence poses well-known challenges in experimental ecology. The most widely recognized of these is that results obtained from small-scale manipulations might not scale up to explain larger-scale patterns. Perhaps equally important, though less widely discussed, is the problem that experimental studies that measure responses at just one spatial scale may capture only a very incomplete picture, and may obtain seemingly idiosyncratic results when in fact a general patterns does exist. We have demonstrated the value of multi-scale sampling to interpreting experimental results, even over relatively small spatial scales. Had we sampled at only one spatial scale, we would have (1) possibly detected no treatment effects at all (e.g. in 1 m^2 plots), (2) failed to detect consistent changes to the SAR induced by the treatments, and (3) not revealed the role of shifts in relative abundance and spatial aggregation in driving treatment effects.

Our results also have implications for the challenge of extrapolating experimental findings to larger spatial scales. Even over the fairly small range of spatial scales considered here, treatment effects on richness were not linear. Thus, there is little reason to hope that extrapolating treatment effects to larger, unmeasured scales would give reasonable estimates. However, it was often the case that treatment effects on richness were largest at small spatial scales. This might suggest that, at least within the 4-yr time scale of this experiment, changes in richness at larger spatial scales might generally be small (but see Crawley et al. 2005 for

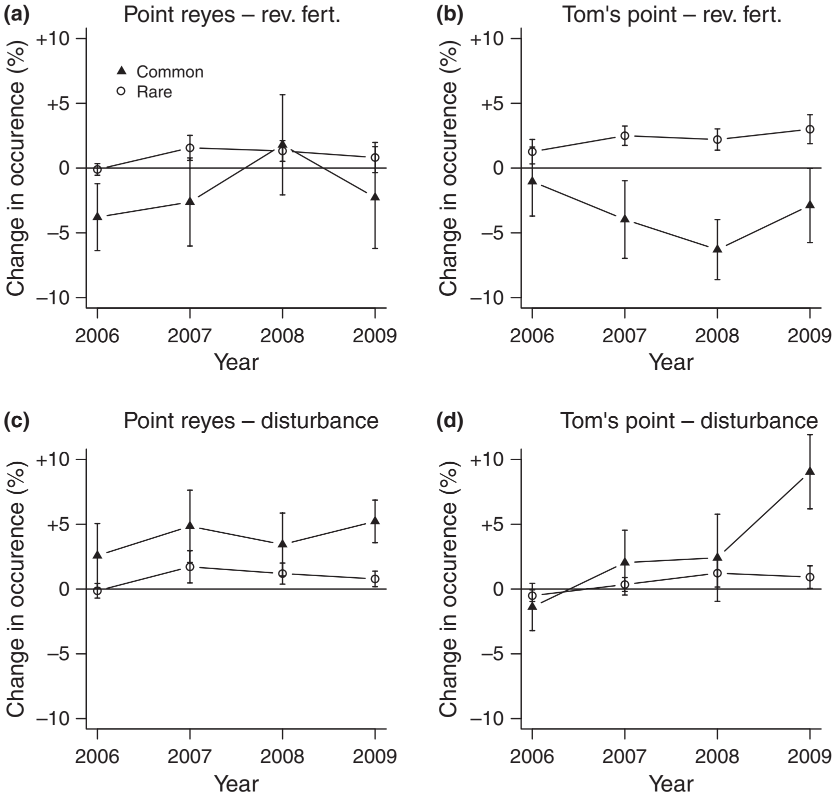

Fig. 4. Differential responses of rare and common species to reverse fertilization (a,b) and disturbance (c,d). Rare species increased in response to reverse fertilization, while common species showed marked decreases, except at Point Reyes in 2008. In contrast, disturbance had no effect on rare species, but made common species even more common. Error bars show standard errors.

richness changes over larger spatial and temporal scales). Supporting this notion, differences in overall richness (total number of species found within all plots of a particular treatment, site and year) among treatments within each site and year were typically < 10%.

Interpretation of treatment effects

Disturbance and reverse fertilization reduced above-ground biomass at both sites, and caused shifts in species relative abundances and spatial aggregation. As a result, these treatments had consequences for the slope of the SAR. This means that both treatment effects were quantitatively scale-dependent. In some cases, reverse fertilization caused reductions of richness at small scales and increases in richness at larger scales, demonstrating that the response of richness to productivity can also be qualitatively scale-dependent. Richness responses at one scale were typically more variable than SAR slope across years and sites. This suggests that changes in the SAR with productivity and disturbance may be more consistent and general than changes in richness at any single scale of measurement.

Changes to the SAR slope took longer to develop than changes in above-ground biomass in response the treatments. Treatment effects on biomass were already evident in 2006, but effects on the SAR in that year were weak or inconsistent with patterns observed later in the experiment. Moreover, both overall biomass and treatment effects on biomass were unusually small in 2009, but strong responses of the SAR were detected in this year. Thus, responses of the community SAR appear to show somewhat more inertia than the relatively rapid response of productivity. This makes sense, because changes in the SAR are driven primarily by population-level responses, while biomass changes can be attributed to changes in growth of individuals. Population-level responses typically take longer to detect than individual responses (Lauenroth & Sala 1992; Shaver et al. 2000; Sandel et al. 2010).

Productivity

Differences in observational scale may explain variable responses of richness to productivity among studies (Mittelbach et al. 2001). Increasing productivity may decrease

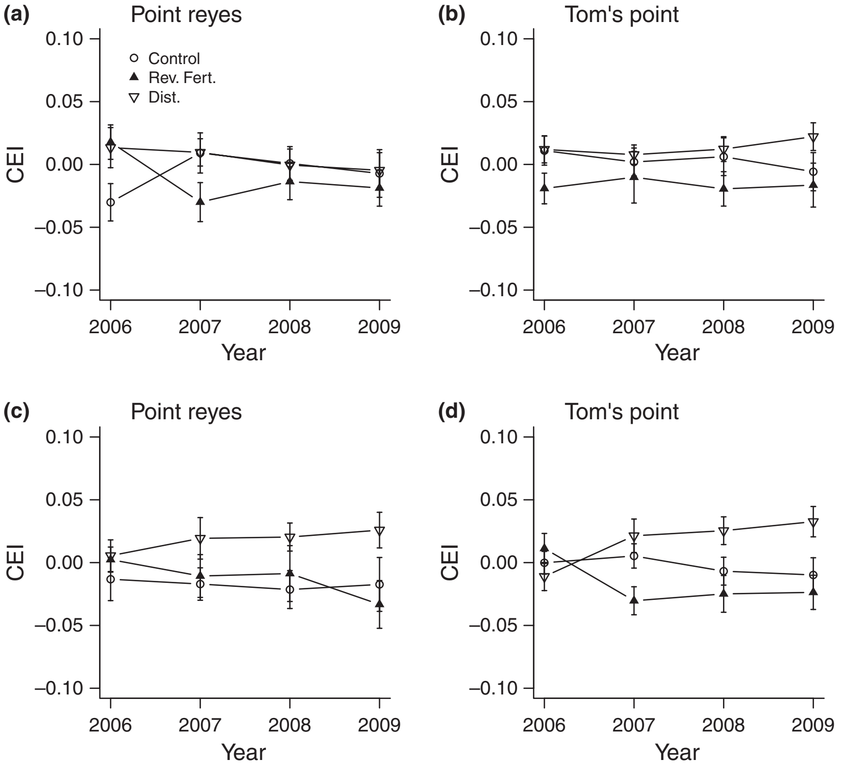

Fig. 5. Changes in community evenness index (CEI), considering the 0.016 m^2 occurrence probabilities, conditional upon occurrence at 0.063 m^2 (**a,b**), or the 0.063 m^2 scale, contingent upon occurrence at 0.25 m^2 (**c,d**). Controlling for intra-specific variation in abundance and tendency to aggregate (see text), species distributions, on average, became more even in disturbance plots. Reverse fertilization at Tom's Point, tended to produce more aggregated spatial distributions. Error bars show standard errors.

richness at small spatial scales (due possibly to competitive exclusion) but increase it at larger scales (due to increases in β-diversity, Chase & Leibold 2002; Chalcraft et al. 2004; Harrison et al. 2006). Similarly, a meta-analysis of experimental fertilization studies found that, while α-diversity was consistently reduced by N fertilization, β-diversity often increased (Chalcraft et al. 2008). This can cause the SARs for control and treatment plots to cross (Dumbrell et al. 2008). Interestingly, we observed the opposite pattern in this study: reduced productivity often reduced species richness in small plots, but increased dissimilarity among small plots produced increases in richness at larger scales. This produces higher SAR slopes, which had previously been observed for *increasing* productivity. A possible explanation for this inconsistency lies in the work of Chalcraft et al. (2008), who noted that increased β-diversity with increased productivity was not universal, but instead depended on the productivity of the site. At sites with > 400 g·ANPP·m^{-2}·yr^{-1}, fertilization tended to decrease β-diversity. The Tom's Point and Point Reyes sites typically produce about 600 g·ANPP·m^{-2}·yr^{-1}, so it is perhaps not surprising that we saw an increase in β-diversity following a decrease in productivity.

A complete understanding of the productivity–diversity relationship may rely on separate understanding of α- and β-diversity patterns. The SAR is a particularly convenient way to think about these patterns, because it does not require an arbitrary division of within- and between-plots, instead treating spatial scale as continuous. Hence, we suggest that the response of the SAR to productivity should become the focus of increased research attention. However, the work of Chalcraft et al. (2008), and the mismatch between our results and some previous work suggest that focusing on the SAR alone might not be sufficient to detect general patterns. Rather, it is likely that a truly general explanation will describe how environmental context determines the response of the SAR slope to productivity changes.

The response of the SAR to reverse fertilization in this study has a clear interpretation, consistent with theoretical expectations. Reducing productivity reduced the occurrence rate of common species (see also Sandel & Corbin 2010), allowing uncommon species to colonize these plots. In some cases, this produced an increase in species richness at the largest scale (2 m × 2 m), as has been seen along other fertility or productivity gradients

Doi: 10.1111/j.1654-1103.2012.01406.x

(e.g. Grime 1973, 1979; Silvertown 1980; Tilman 1993). In other cases, the increased abundance of rare species and decreased occurrence rate of common species resulted in no or small overall changes in species richness at large scales. Two factors led to steeper SAR slopes with reverse fertilization. First, species distributions became more aggregated (Fig. 5); second, the reduced abundance of common species (and a corresponding increase in bare ground, Sandel et al. 2011) reduced species richness at the smallest spatial scales. This reduction in abundance of common species may reflect the fact that soils at these sites have anthropogenically elevated *N* availability, causing species that are adapted to high *N* to be initially abundant.

Disturbance

The reduction of the SAR slope with increased disturbance is consistent with previous observational results at larger scales for lepidopterans (Hamer & Hill 2000; Hill & Hamer 2004; Dumbrell et al. 2008), but opposite to patterns observed for birds (Hill & Hamer 2004). One proposed explanation for this reduced SAR slope is that, while disturbance creates opportunities for species that would otherwise be excluded from the community, increasing small-scale richness, it also homogenizes habitats, reducing large-scale richness (Dumbrell et al. 2008). This is consistent with the mechanisms detected in this study. Richness at the smallest scale did increase with disturbance, as theory (Connell 1978; Huston 1979) would predict; however, the increased spatial evenness of species distributions led to less between-subplot β-diversity, reducing the SAR slope. Interestingly, the increased abundance of already common species observed in disturbed plots also mirrored changes in species abundance of lepidopterans in logged forests (Hamer & Hill 2000).

The observed increase in the evenness of species distributions probably reflects the removal of small-scale heterogeneity by the disturbance treatment. Small-scale structure in canopy openness and vegetation height likely contribute to patchy species distributions in control plots; removal of this structure led to even distributions and shallower SARs. Already-common species benefitted from the disturbance treatment which, like their negative response to the reverse fertilization treatment, is probably because many of the common species at the site are weedy exotic species that are able to rapidly capitalize on increases in resource availability caused by disturbance.

Because clippings were removed from plots after mowing, this treatment also caused an export of nutrients from plots over time. This reduction in fertility due to the disturbance treatment was likely to be small relative to that due to the reverse fertilization treatment (Sandel et al. 2011).

Variation among sites and years

The two sites differed substantially in overall species richness, with Tom’s Point typically showing about 70% higher richness (in 1 m × 1 m plots) than Point Reyes. This likely relates to different land-use histories. Tom’s Point may have been used for some crops, but the Point Reyes site was certainly managed more intensively. As a result, there are a number of native species found at Tom’s Point but not Point Reyes. Overall differences in richness between the sites may have influenced measured treatment effects. Proportional changes in species richness were similar between the two sites (Figs 1 and 2), indicating that the absolute changes in species richness were larger at Tom’s Point than at Point Reyes, as predicted (Huston 1999).

There was a slightly negative relationship between species richness (at 1 m × 1 m) and productivity within a particular site and year (Fig. S3), consistent with expectations (Huston 1979, 1999). However, this overall relationship did not predict the change in species richness induced by a particular treatment very well, perhaps indicating that treatments altered species richness through additional mechanisms besides altering productivity. Overall productivity was unusually low in 2009. That year, the responses of the SAR to reverse fertilization were also rather weak (Figs 1 and 2). In the winter of 2008–2009, heavy precipitation began unusually late in the year, with the first major events occurring in February (as opposed to December or January in previous years, PRISM Climate Group, Oregon State University 2010). This may explain both the reduced overall biomass and the reduced magnitude of reverse fertilization treatment effects in 2009. It is also possible that productivity in the control plots had fallen so much in 2009 that further reduction would be expected to reduce species richness rather than increase it (e.g. Al-Mufti et al. 1977). Interestingly, while the low biomass production of 2009 was associated with weak reverse fertilization treatment effects, disturbance had the strongest positive effects on richness and greatest scale dependence in that year. This supports the idea that productivity was not limited by *N* availability in 2009, but possibly by water availability. Thus, reverse fertilization had small effects, while mowing impacts the community regardless of what is ultimately limiting plant growth.

Scale dependence and the SAR

These results illustrate the complexity of responses of species richness to experimental manipulation. The fundamental difficulty arises from the fact that changes at a particular spatial scale cannot be unequivocally attributed to any particular factor. They could be due to changes in richness at a larger scale, changes in species' spatial aggregation or changes in the species abundance distribution. With multi-scale sampling, however, these factors can be separated, yielding a clearer understanding of richness changes (Tittensor et al. 2007). Hence, we suggest that asking how species richness responds to certain factors is unlikely to be as informative as asking how the SAR responds (Pastor et al. 1996; Weiher 1999).

Much research (Waide et al. 1999; Mackey & Currie 2001; Mittelbach et al. 2001) has disagreed on the form of the productivity–diversity and disturbance–diversity relationships. One likely source of disagreement is that studies are performed at different spatial scales (Chase & Leibold 2002; Harrison et al. 2006; Dumbrell et al. 2008). We confirmed that the response of species richness to variation in productivity and disturbance is scale-dependent, even at the relatively small scales examined here. This supports the idea that a complete understanding of these relationships will require continued work that examines effects at multiple scales. Cross-scale studies, in general, facilitate comparisons by increasing the likelihood that two studies will measure a property at a comparable spatial scale, while also revealing when mismatches in scale are a likely culprit for disagreements of ecological results. In contrast, if one suspects a particular pattern may be scale-independent, cross-scale studies such as this can confirm that conjecture, perhaps revealing a very general pattern.

Finally, because SARs provide a fundamentally more nuanced and complete description of species richness than do measurements at a single spatial scale, explanations of treatment effects on SARs may also be more comprehensive. This study revealed some of the mechanistic basis for changes in species richness across scales. Co-ordinated changes in species abundance distributions and spatial patterns can cause treatment effects to be scale-dependent in ecological experiments.

Acknowledgements

Many thanks to the numerous assistants that made the fieldwork possible. We appreciate the exceptional support of the Audubon Canyon Ranch and the Point Reyes National Seashore. Particular thanks go to John DiGregoria. Wayne Sousa, David Ackerly, John Harte, Michael Huston, members of the Sousa lab at UC Berkeley and two anonymous reviewers provided helpful comments on the manuscript. B.S. was supported by an NSF predoctoral fellowship, and by grants from the Robert and Nancy Beim Research Fund and the Gray Endowment.

References

Aerts, R. & Berendse, F. 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathland. *Vegetatio* 76: 63–69.

Allcock, K.G. & Hik, D.S. 2003. What determines disturbance–productivity–diversity relationships? The effect of scale, species and environment on richness patterns in an Australian woodland *Oikos* 102: 173–185.

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* 65: 759–791.

de Bello, F., Lepš, J. & Sebastiá, M.-T. 2007. Grazing effects on the species–area relationship: variation along a climatic gradient in NE Spain. *Journal of Vegetation Science* 18: 25–34.

Bossuyt, B. & Hermy, M. 2004. Species turnover at small scales in dune slack plant communities. *Basic and Applied Ecology* 5: 321–329.

Carey, S., Harte, J. & del Moral, R. 2006. Effect of community assembly and primary succession on the species–area relationship in disturbed ecosystems. *Ecography* 29: 866–872.

Chalcraft, D.R., Williams, J.W., Smith, M.D. & Willig, M.R. 2004. Scale dependence in the species richness–productivity relationship: the role of species turnover. *Ecology* 85: 2701–2708.

Chalcraft, D.R., Cox, S.B., Clark, C., Cleland, E.E., Suding, K.N., Weiher, E. & Pennington, D. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology* 89: 2165–2171.

Chase, J.M. & Leibold, M.A. 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416: 427–430.

Chesson, P., Donahue, M.J., Melbourne, B.A. & Sears, A.L. 2005. Scale transition theory for understanding mechanisms in metacommunities. In: Holyoak, M., Leibold, M.A. & Holt, R.D. (eds.) *Metacommunities: spatial dynamics and ecological communities*, pp. 279–306. University of Chicago Press, Chicago, IL, US.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

Crawley, M.J., Johnston, A.E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M.S., Henman, D.F. & Edwards, G.R. 2005. Determinants of species richness in the park grass experiment. *The American Naturalist* 165: 179–192.

Drakare, S., Lennon, J.L. & Hillebrand, H. 2006. The imprint of geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters* 9: 215–227.

Dumbrell, A.J., Clark, E.J., Frost, G.A., Randell, T.E., Pitchford, J.W. & Hill, J.K. 2008. Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. *Journal of Applied Ecology* 45: 1531–1539.

Ellis, J. & Schneider, D.C. 2008. Spatial and temporal scaling in benthic ecology. *Journal of Experimental Marine Biology and Ecology* 366: 92–98.

Doi: 10.1111/j.1654-1103.2012.01406.x

Francis, A.P. & Currie, D.J. 2003. A globally consistent richness–climate relationship for angiosperms. *The American Naturalist* 161: 523–536.

Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89: 428–439.

Grime, J.P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1: 151–167.

Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley, New York, NY, US.

Hamer, K.C. & Hill, J.K. 2000. Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* 14: 1435–1440.

Harrison, S., Davies, K.F., Safford, H.D. & Viers, J.H. 2006. Beta diversity and the scale-dependence of the productivity–diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology* 94: 110–117.

Harte, J., Conlisk, E., Ostling, A., Green, J.L. & Smith, A.B. 2005. A theory of spatial structure in ecological communities at multiple spatial scales. *Ecological Monographs* 75: 179–197.

Harte, J., Zillio, T., Conlisk, E. & Smith, A.B. 2008. Maximum entropy and the state-variable approach to macroecology. *Ecology* 89: 2700–2711.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J., Kaufman, D., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. 2003. Energy, water and broad-scale geographic patterns of species richness. *Ecology* 84: 3105–3117.

He, F. & Legendre, P. 2002. Species diversity patterns derived from species–area models. *Ecology* 83: 1185–1198.

Hewitt, J.E., Thrush, S.F., Dayton, P.K. & Bonsdorff, E. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. *The American Naturalist* 169: 398–408.

Hickman, J.C. (ed.). 1993. *The Jepson manual: higher plants of California*. Univeristy of California Press, Berkeley and Los Angeles, CA, US.

Hill, J.K. & Hamer, K.C. 2004. Determining impacts of habitat modification on tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41: 744–754.

Huston, M.A. 1979. A general hypothesis of species diversity. *The American Naturalist* 113: 81–101.

Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393–401.

Kaiser, M.J. 2003. Detecting the effects of fishing on seabed community diversity: importance of scale and sample size. *Conservation Biology* 17: 512–520.

Lauenroth, W.K. & Sala, O.E. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397–403.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Levine, J. & D'Antonio, C.M. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87: 15–26.

Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist.* 10: 17–25.

Mackey, R.L. & Currie, D.J. 2001. The diversity–disturbance relationship: Is it generally strong and peaked? *Ecology* 82: 3479–3492.

Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13: 261–265.

Pastor, J., Downing, A. & Erickson, E. 1996. Species–area curves and diversity–productivity relationships in Beaver Meadow of Voyageurs National Park, Minnesota, USA. *Oikos* 77: 399–406.

PRISM Climate Group, Oregon State University. 2010. 800m Normals. http://prism.oregonstate.edu/

Reichle, D.E. (ed.). 1970. *Analysis of temperate forest ecosystems*. Springer, New York, NY, US.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 167–171.

Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.

Sandel, B. & Corbin, J.D. 2010. Scale, disturbance and productivity control the native–exotic richness relationship. *Oikos* 119: 1281–1290.

Sandel, B. & Smith, A.B. 2009. Scale as a lurking factor: incorporating scale-dependence in experimental ecology. *Oikos* 118: 1284–1291.

Sandel, B., Goldstein, L.J., Kraft, N.J.B., Okie, J.G., Shuldman, M.I., Ackerly, D.D., Cleland, E.E. & Suding, K.N. 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist* 188: 565–575.

Sandel, B., Corbin, J.D. & Krupa, M. 2011. Using plant functional traits to guide restoration: a case study in California coastal grassland. *Ecosphere* 2: 1–16. article 23.

Schlesinger, W.H. 1997. *Biogeochemistry: an analysis of global change*. Academic Press, San Diego, CA, US.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, G., Harte, J., Henry, G., Ineson, P., Melillo, J., Pitelka, L. & Rustad, L. 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50: 871–882.

Silvertown, J.W. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the park grass experiment. *Journal of Applied Ecology* 17: 491–504.

Šizling, A. & Storch, D. 2004. Power-law species–area relationships and self-similar species distributions within finite areas. *Ecology Letters* 7: 60–68.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60: 1225–1239.

Storch, D., Šizling, A., Reif, J., Polechová, J., Šizlingová, E. & Gasoton, K.J. 2008. The quest for a null model for macroecological patterns: geometry of species distributions at multiple spatial scales. *Ecology Letters* 11: 771–784.

Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179–2191.

Tittensor, D.P., Micheli, F., Nyström, M. & Worm, B. 2007. Human impacts on the species–area relationship in reef fish assemblages. *Ecology Letters* 10: 760–772.

Tjørve, E., Kunin, W.E., Polce, C. & Tjørve, K.M.C. 2008. Species–area relationship: separating the effects of species abundance and spatial distribution. *Journal of Ecology* 96: 1141–1151.

Tylianakis, J.M., Klein, A.-M., Lozada, T. & Tscharntke, T. 2006. Spatial scale of observation affects α, β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. *Journal of Biogeography* 33: 1295–1304.

Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30: 257–300.

Weiher, E. 1999. The combined effects of scale and productivity on species richness. *Journal of Ecology* 87: 1005–1011.

Whittaker, R.J., Willis, K.J. & Field, R. 2001. Scale and species richness: towards a general hierarchical theory of species diversity. *Journal of Biogeography* 28: 453–470.

Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

Willis, K.J. & Whittaker, R.J. 2002. Species diversity – scale matters. *Science* 295: 1245–1248.

Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Unstandardized SARs for Point Reyes.
Figure S2. Unstandardized SARs for Tom's Point.
Figure S3. Biomass–richness relationships.