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Empirical and theoretical approaches to understanding diversity
patterns across multiple spatial scales

By

Brody Steven Sandel

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Wayne P. Sousa, Chair

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patterns across multiple spatial scales

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Abstract

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Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Wayne P. Sousa, Chair

Patterns of variation in species richness are some of the oldest known ecological phenomena. Centuries of research into their causes have revealed surprisingly few general insights, one of which is that the factors that control richness depend on spatial scale. At large spatial scales, processes such as dispersal, speciation and extinction are thought to be most important, while biological interactions can be important at small spatial scales. The abiotic environment affects all of these processes. For example, high temperatures can promote speciation, while small-scale environmental heterogeneity can slow competitive exclusion. I am interested in controls on species richness across all spatial scales, and in understanding how processes at one scale impact processes at other scales. Accordingly, my research has spanned a vast range of scales, from field sampling plots as small as 0.016 m^2 to maps of richness patterns across the entire New World. I have employed a correspondingly diverse range of approaches, as appropriate to each spatial scale. Through a combination of modeling and experimental research, my research has helped to illuminate the factors that control variation in richness, and, critically, to reveal how these controls change at different spatial scales.

For Esther

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Introduction

Species richness, the number of species occurring in a particular sample, is an important characteristic of ecological systems. For at least 150 years, biologists and ecologists have documented patterns of variation in species richness and sought to explain them (e.g. Darwin 1859, Wallace 1876). One of the longest recognized ecological patterns is the latitudinal richness gradient in which, for most taxonomic groups, richness declines as one travels from the tropics to the poles (Rosenzweig 2005, Hillebrand 2004). The generality of this pattern across many species groups suggests that it could have a similarly general explanation. However, even after decades of research, there is still no consensus on the cause of the latitudinal richness gradient (Pianka 1966, Rohde 1992, Rosenzweig 1995).

At smaller scales, there are many other common patterns of species richness that require explanation. Elevational gradients are common; one often observes a decline of richness at high elevations (Lomolino 2001). Within particular communities, richness may be influenced by soil conditions (e.g. nutrient availability, soil moisture), topographic heterogeneity or microscale variation in climate. Finally, of course, richness is influenced by direct and indirect interactions among species. The presence and abundance of predators, competitors, pathogens, mutualistic partners and ecosystem engineers can all have strong influences on the richness of a group (Huston 1979).

One intriguing property of species richness is that its controls vary as a function of spatial scale (Wiens 1989, Levin 1992, Mittelbach 2001, Whittaker et al. 2001, Sandel and Smith 2009). A particular factor, such as productivity, can have very different relationships with species richness, depending on the scale of observation (Mittelbach et al. 2001). As a result, interpretations of richness patterns vary with scale (Rahbek and Graves 2001, Hurlbert and White 2005).

This scale-dependence fascinates me. It is the unifying theme of this dissertation, in which I address causes of variation in species richness across a wide range of scales. I begin with consideration of continental-scale patterns of species richness. Because of the large scale of these inquiries, I take a modeling approach in this section. Then, I turn to small-scale richness patterns, asking how species richness responds to experimental restoration treatments in coastal Californian grasslands, across a range of spatial scales. Finally, I ask whether a particular restoration treatment is a viable tool to reintroduce native diversity to heavily invaded Californian grasslands.

The first two chapters of this dissertation concern the effect of geometry on species richness patterns. This line of inquiry was opened in 1994, in an important article by Colwell and Hurtt. In it, they showed that randomly placing species ranges within bounded domains (such as continents or islands) can lead to non-uniform patterns of richness. Typically, random placement models (called geometric constraint models, or GCMs) predict a maximum of species richness in the middle of the domain. In the first chapter I make explicit the assumptions that lead to this effect, and argue that the model that predicts a uniform richness pattern is most consistent with what we know about species ranges. Intriguingly, though, even this model predicts non-uniform patterns of other range parameters, such as range size and shape. Thus, geometric constraints, even if they do not directly affect richness, do have effects on other characteristics of species' ranges.

In the second chapter, I take advantage of these effects. I argue that progress on geometric constraint models has been stymied by a lack of agreement on which models to use.

Many models have been developed, but there has been little discussion of why one should be selected over another. I believe that this is partially due to the fact that no methods have yet been proposed to make between-model comparisons based on fit to data. In this chapter, I suggest such a method, and demonstrate it by comparing predictions of three models for patterns of richness, range area and range shape to empirical patterns for all New World birds and mammals. I show that the best-performing model depends on the range size of the group in question.

I then turn to small-scale patterns of species richness. Experiments are useful tools to illuminate mechanistic bases for species richness patterns, but in most cases are only feasible at relatively small spatial scales. Most experimental studies measure responses to manipulations at only one spatial scale. While convenient, this hampers comparison and generalization, as other studies likely made measurements at different spatial scales. Furthermore, it is possible for results to differ qualitatively, depending upon the scale at which they were measured. I investigated this possibility by examining responses of plant species richness to experimental restoration treatments across five spatial scales. Indeed, the degree and even the direction of the effect of these treatments on species richness were scale-dependent. By collecting data across multiple spatial scales, I was also able to show more clearly the mechanisms leading to the observed changes in species richness.

In the final chapter, I address an applied problem related to species richness, that of biological invasions. Many plant communities across the world have been affected to various degrees by the arrival of non-native species, but few have been as thoroughly impacted as the California grasslands. Across the state, there has been widespread replacement of native grassland species with their exotic counterparts, which often originated in Europe. This has caused substantial declines in native species richness across a wide range of scales. I examined a restoration treatment, called reverse fertilization, as a potential tool to restore native richness to California's grasslands. While the treatment has been reasonably successful elsewhere in California, it did not increase native richness or abundance at the two sites where I tested it. However, I measured a suite of plant traits, and demonstrate that these traits allow better predictions of species' responses.

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When I got to Berkeley, I found myself in the exceptionally qualified hands of Wayne Sousa. Over the course of my six years in his lab, we have had innumerable conversations that defined my dissertation. Certainly, no one else has been as influential in determining how I think about ecology and approach research, and I consider myself extremely lucky to have had Wayne's influence. Wayne has also been an incredibly supportive and kind advisor. He has believed in the value of my research (or at least pretended to!) when I was unsure, and taken a genuine interest in my life, happiness and well-being.

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Chapter 1
Reconsidering null models of diversity:
Do geometric constraints on species ranges
necessarily cause a mid-domain effect?

Abstract

Recent null models that place species ranges randomly within a bounded domain have been controversial. Many such geometric constraint models predict a peak in species richness in the center of domains in the absence of underlying environmental gradients or interspecific interactions. I used two-dimensional simulation models to explore different ways that species ranges could interact with the domain boundary. In the rejection model, a randomly generated range that overlaps a domain boundary is removed from the simulation. In the reshaping model, a range that overlaps the domain boundary is reshaped so that the entire range is placed within the domain. The truncation model allows potential ranges to extend across the boundary, but only that portion of the range within the domain is included in the realized range. Both rejection and reshaping models produced a decline in species richness near domain boundaries, though the effect was less pronounced in the reshaping model. The truncation model did not produce any spatial pattern in species richness. Thus, particular assumptions made regarding range placement at the domain boundary determine whether or not a mid-domain effect is obtained.

Range truncation is consistent with bioclimate envelope models, which can successfully predict a species' range in response to the availability of appropriate climate conditions. I argue that it is therefore more realistic to assume flexible, rather than fixed, range sizes. Other range characteristics, including size and shape, can change near domain boundaries in the null models, including the truncation model. A broader consideration of range characteristics near domain boundaries could be productive.

Introduction

The cause of large-scale spatial patterns in species richness remains one of the great unexplained problems in macroecology (Brown 1995, Blackburn and Gaston 2003). Perhaps the best-known such pattern is the latitudinal gradient in diversity, which has been called "ecology's longest recognized pattern" (Willig et al. 2003). Yet after many decades of investigation, there remains a complex array of competing hypotheses that have yet to yield an explanation for the latitudinal gradient (Willig et al., 2003).

Colwell and Hurtt (1994) proposed a novel approach to the problem of the spatial distribution of species richness, based on geometric constraints on the arrangement of species ranges within a bounded domain. One surprising prediction of such geometric constraint models is that the random placement of species onto a spatially constrained domain can cause gradients in species richness, including a peak in the middle of the domain (reviewed in Zapata et al. 2003, Colwell et al. 2004). Despite its supposed status as a null model, geometric constraints have been interpreted as a primary cause of observed species richness patterns in some cases (e.g. Willig and Lyons 1998, Lees et al. 1999, Jetz and Rahbek 2001, McCain 2003, McCain 2004, Romdal et al. 2005). Other data sets do not seem to fit the predictions of geometric constraint models (Koleff and Gaston 2001, Hawkins and Diniz-Filho 2002, Laurie and Silander 2002, Kerr et al. 2006).

There are strongly divergent views on the usefulness of geometric constraint models (Zapata et al. 2003, Colwell et al. 2004, Hawkins et al. 2005). One source of controversy has been the assumptions and methods of constructing a null model of species distributions in a geometrically constrained domain. As emphasized by Gotelli (2001), there is no single null model that can be considered correct, and it is necessary to consider multiple approaches to the

construction of null models. Here I suggest that most previous treatments of geometric constraint models are based on a particular method of randomly placing species within a bounded domain, and that a reasonable alternative causes the mid-domain effect to disappear.

What happens at the hard boundary?

If species ranges are placed at random on a globe without geographical features, then no spatial pattern in species richness is expected (Colwell and Hurtt 1994, Grytnes 2003). Any spatial variation in diversity results only from the stochastic process of placing a finite number of ranges on the globe.

The situation becomes more complex when the globe is divided into discrete regions within which organisms are placed by a randomization procedure. For example, continents and oceans might be designated, and the placement of terrestrial organisms then would be constrained to occur within the continental domain. Such a continental edge is an example of a hard boundary (Colwell and Hurtt 1994). Less drastic differences in habitat, such as between forest and grassland, could also define the boundaries of a domain; see Colwell et al. (2004) for a discussion of the nature of biologically relevant boundaries.

What properties of hard domain boundaries would cause spatial patterns in species richness to arise in a null model? The fundamental question is how to place species ranges at random within a bounded domain. I consider three approaches to the boundary problem.

Range rejection

There are two characteristics that must be chosen for each species in the process of placing its range randomly within a bounded domain: range size and range location (fig. 1a). In the rejection model, once a range size is selected, only locations that allow a range of the chosen size to be placed entirely within the domain are allowed. Any location that causes the range to overlap the domain boundary is rejected (fig. 1b).

Many previous models for geometric constraints implicitly adopt the rejection approach for hard boundaries (e.g. model 2 of Colwell and Hurtt 1994). These models usually do not formally place ranges at all locations and then discard those that cross domain boundaries. Rather, once a range size is chosen for a species, placement of that range is constrained to occur only where it will fit entirely within the domain. Species with small ranges can be located in many places in the domain, but species with large ranges must be centered near the middle of the domain. Thus, compared to a model without domain boundaries where a range of any size can occupy any location, most geometric constraint models effectively reject the placement of some ranges near the boundary.

Range reshaping

As in rejection models, the first step in a reshaping model is the selection of a range size at random and the second step is the random choice of a location for the range. But if the resulting range crosses a boundary, the range is reshaped to maintain its overall size but fit it into the domain boundaries (fig. 1c).

There are a number of ways ranges could be reshaped to fit within domain boundaries. One approach has been to create two-dimensional ranges by a process analogous to a liquid dye spreading over a flat surface (Jetz and Rahbek 2001, Kerr et al. 2006). In such “spreading dye” models, the process of range placement begins by selecting a random starting grid cell within a gridded domain. The range is allowed to expand at random into adjacent cells until the range has

reached its designated size. Ranges are not allowed to expand to cells outside the domain. Thus the restriction of range expansion at the boundary has the effect of changing the range's shape, relative to its shape were the boundary not present.

Range truncation

A third possibility, range truncation, has not been seriously explored in most previous geometric constraint models. If a randomly generated range size and location results in a range that crosses the domain boundary, only that portion of the range outside the domain is discarded (fig. 1d). The realized range is then smaller than that designated by the random selection of range size, and the midpoint of the realized range is shifted away from the boundary.

The truncation method was inspired by bioclimate envelope models of species ranges, in which the range of a species is determined by the set of climatic conditions within which a species can maintain a population (reviewed in Pearson and Dawson, 2003). Such models have been used to predict how species ranges will change in response to impending climate change (e.g. Peterson et al. 2002, Williams et al. 2003, Thomas et al. 2004, Kueppers et al. 2005). The realized range of a species is not a constant, but is a flexible response to the availability of the area of appropriate climate conditions within a domain (Hawkins and Diniz-Filho, 2002; Hawkins et al., 2005).

In a truncation model, the choice of a random range size and location can be considered equivalent to the choice of a random set of climatic conditions within which a species can exist. If those conditions extend beyond the domain boundary, the species only occupies that portion of the range within the domain.

Simulations

I used Monte Carlo simulations to compare rejection, reshaping, and truncation approaches to random range placement within a bounded domain. Simulation programs were written in C++.

The core model is similar to the “spreading dye” geometric constraints model of Jetz and Rahbek (2001), which produces a two-dimensional continuous range of a given size by incremental additions to a random starting point. I focus on two-dimensional ranges because important characteristics of ranges and their distribution cannot be captured by one-dimensional abstractions of ranges (Jetz and Rahbek, 2001; Zapata et al., 2003; Hawkins and Diniz-Filho, 2004).

The domain in my simulations was defined as a square grid of 48×48 cells. A single cell is defined as the minimum size that will support a viable population of the species being placed on the domain. This minimum area undoubtedly varies widely among organisms, but for domains of continental scale this area is probably large enough to maintain populations of most organisms. For example, if Africa is divided into 2304 (i.e. 48×48) cells, each would be c. 13,000 km². This is the equivalent of approximately half of the Serengeti ecosystem as defined by the annual wildebeest migration, surely large enough to maintain populations of most species. The number of cells could be adjusted in the model to accommodate different types of organisms or different sizes of domains, but this has little effect on the outcome of the simulations.

To add a species to the domain, a range size (total number of cells to be occupied) was chosen at random from a uniform distribution. I have also run simulations with other range size frequency distributions (e.g. lognormal), and the results were qualitatively similar to those

presented here for a uniform distribution. To determine the effect of varying the average size of ranges relative to the domain, I used mean range sizes of 5, 10, 20, and 40% of the entire domain. The range sizes were chosen from a uniform distribution between 50 and 150% of the mean range size.

To place a range within the domain, a starting cell was chosen randomly from the grid. The range was then expanded one cell at a time until the predetermined range size was reached. Except at the domain boundary, cells were added by randomly picking any one of the unoccupied squares adjacent to the current range. Thus, species were forced to have continuous ranges, but range shape was two-dimensional and potentially complex. I used variations of this basic approach to assess the impact of changing assumptions about how ranges interact with domain boundaries (fig. 1).

For the rejection model, I allowed the addition of new cells whether they were inside or outside the domain. However, if a cell outside of the domain was added to the range by random selection, that range placement was rejected, and a new location and size was generated for the species. This continues until the range is placed successfully entirely within the domain.

For the reshaping model, I modified the way cells were added to ranges. New cells were chosen only from the adjacent cells that were within the domain, so the range could not expand past the domain boundary.

For the truncation model, ranges were allowed to expand at random as described above. In this case the domain boundary was ignored until growth of ranges was complete. Ranges were allowed to expand beyond the domain boundary. Starting cells could be outside the boundary, since ranges starting beyond the boundary sometimes grew to include cells within the domain. After the range was complete, portions of the ranges outside the domain were removed and only within-domain portions were used for further analysis.

To determine the effect of changing assumptions about domain boundaries on species richness, I placed 200 species within the domain, and tallied species richness in each of the 48 rows of the square domain. This is equivalent to choosing either latitude or longitude for analysis, as in most previous literature. The random placement of 200 species constituted a model run, which were replicated 100 times for each model type and mean range size (5, 10, 20 or 40% of the domain area).

I also addressed patterns of range area and range shape, using a single placement of 10,000 species with a mean range size of 20% of the domain, for each model. Patterns of range shape were assessed using the relationship of the row number of a species' range midpoint (see below) to its range shape, where shape is defined as the number of columns occupied by the species to the number of rows occupied by it. To examine how range size varied with domain position, I used the mean range size of all species present at a particular location ('Stevens plots', after Stevens, 1989).

The midpoint of a range was defined as its geographical center. For each dimension (latitude and longitude), the midpoint is the average of the value of all quadrats within the range. The midpoint generally would not be the same as the randomly chosen starting point for the range, although on average these two points would be close to each other (except near the domain boundaries, particularly in the reshaping and truncation models).

Results

The rejection, reshaping, and truncation models showed very different patterns of species richness within the bounded domain (fig. 2). The rejection and reshaping models produced decreases in richness near the domain boundaries, and showed a mid-domain peak in richness when range sizes were sufficiently large. However, in the truncation model there was no gradient of species richness within the bounded domain.

Though both the rejection and the reshaping models predict lower richness near the domain boundary, the impact on richness was generally less pronounced in the reshaping model. In the rejection model, richness fell to 5–10% of the maximum observed value in the domain as the boundary was approached. Boundary richness remained higher in the reshaping model, dropping only to about 45% of the observed maximum.

In the rejection and reshaping models, there was no effect of position within the domain on mean range size (fig. 3). However, in the truncation model, the average range size decreased by approximately half as the domain boundary was approached (fig. 3). The truncation model also produced smaller range sizes overall (fig. 3), as a result of the process of range truncation at the boundary.

Range shape became skewed near the domain boundary for the truncation and reshaping models (fig. 4). For midpoints near the boundary, average range length (parallel to the boundary) approached twice the value of the average range width (perpendicular to the boundary). There was only a slight change in shape of ranges in the rejection model.

Discussion

Clearly there are ways to place species ranges randomly within a bounded domain that do not lead to mid-domain effects or other non-uniform spatial patterns in species richness. The rejection and reshaping models produced large changes in species richness across the domain, with reduced richness near domain boundaries. In contrast, the truncation model showed no change in species richness across the domain. Some previous treatments have considered truncation models in one dimension (e.g. model 1 of Colwell and Hurtt 1994, model 0 of Grytnes and Vetaas 2002), and also found no change in species richness within bounded domains.

Many previous null models of species distribution within bounded domains have found a decrease in richness near the boundary (Colwell and Hurt 1994, Willig and Lyons 1998, Jetz and Rahbek 2001, Grytnes 2003, Connolly 2005, Rangel and Diniz-Filho 2005, Romdal et al. 2005), as I found for both rejection and reshaping models. This species richness pattern probably will occur in any model in which 1) the range size is chosen at random (either from a specified distribution or by sampling from a list of real range sizes), and 2) the range of the specified size is placed at random within the regions of the domain where they will fit (Colwell et al. 2004). A critical assumption of such models is that the range size is an inflexible characteristic assigned to a species at random. Once a range size is assigned to a species, it must be placed into the domain where it can fit. As a result, species with large ranges are less common near domain boundaries. For a useful physical analogy, see Colwell et al.'s (2004) description of pencils of various length (analogous to ranges) being shaken in a pencil box (analogous to the bounded domain). Pencils cannot change size, but only position within the pencil box.

Alternatively, the truncation model assumes that the actual range of a species is a flexible response to the availability of appropriate habitat. The randomization steps (assignment of a

range size and location) are analogous to the assignment of a climate envelope within which the species can potentially exist. The realized range is determined by how much of the potential range actually exists within the domain. Hawkins and Diniz-Filho (2002) and Hawkins et al. (2005) have argued persuasively that range sizes should not be considered unchanging characteristics of a species, but rather a flexible response to the location of appropriate conditions within available habitats.

This view of ranges is supported by the success of bioclimate envelope models in explaining the current distribution of species and in predicting how they will respond to climate change. It has long been known that the size and position of species ranges responded rapidly to Holocene climate changes (Huntley and Webb 1989, Prentice et al. 1991). For example, the range of a species such as white spruce (*Picea alba*) has changed dramatically in North America as glaciers have advanced and retreated (Williams et al. 2001). Presumably, this species has retained similar ecological and physiological characteristics throughout this time, but the realized range at any time was determined by the distribution of the bioclimate envelope within which the species could survive. It is likely that at times some of white spruce's bioclimate envelope extended beyond the continental boundary, and was therefore unoccupied.

The essential difference between the truncation model and many previous bounded-domain models is the nature of the geometric constraint imposed by the boundary. Clearly ranges in all three models are constrained by the domain boundary, since no species is distributed outside the domain (fig. 1). In rejection and reshaping models, the boundary imposes a constraint on how a range of constant assigned size can fit within a domain. In the truncation model, the boundary imposes a constraint on how large the realized range of a species will be given an assigned bioclimate envelope.

Given the flexibility of range sizes of real species, it seems unnecessarily artificial to treat range size as a fixed characteristic assigned to a species. If the effect of hard boundaries is to truncate potential species ranges, then there is no richness pattern within bounded domains. Thus, I do not support the suggestion that bounded domains inevitably cause changes in species richness in null models.

Predictions from the models: What variables change at hard boundaries?

In the truncation model, there is no decline in species richness near domain boundaries, as occurs in the other two models. However, the truncation model predicts that other variables should change as domain boundaries are approached, and examination of these variables should help in assessing the usefulness of the various models. Previous treatments of the effects of hard boundaries often have been described as “mid-domain” effects. This can be misleading, since the changes in response variables sometimes occur only relatively near the boundary and do not extend to the center of the domain (Laurie and Silander 2002, Zapata et al. 2003, see figs 2, 3, and 4). Thus, I prefer to call these responses boundary effects.

There are boundary effects on characteristics other than species richness. In the truncation model, range size is reduced near the boundary and the overall range size is smaller than in the rejection and reshaping models (fig. 3). All three models used the same starting distribution of range sizes. In the reshaping model, the distribution of range sizes closely matched the starting uniform distribution. This is because every species that is generated by the reshaping model will occupy the range specified, even though this may require a change in shape. In the rejection model, the mean of the realized range size distribution is smaller than the starting distribution, because the probability of a range being rejected increases with its size. In the

truncation model, the observed ranges were strongly skewed toward smaller sizes because range sizes were reduced if they crossed the domain boundary. Interestingly, most empirical data on range size frequency distributions also show a mode at the smallest range size when expressed on an arithmetic scale (Brown et al. 1996, Gaston 2003, Lyons 2005). Though there has been more focus on the impact of various bounded-domain models on species richness rather than range size frequency distributions, Arita (2005) has emphasized the impact of geometric constraints on range sizes in both one- and two-dimensional models.

Two of these models predict that range shape will change as hard boundaries are approached (fig. 4). Only a very slight shape effect is seen in the rejection model. Near a hard boundary, both the reshaping and the truncation models produce ranges that are extended in length (parallel to the boundary) relative to width (perpendicular to the boundary). In the reshaping model, the greater range length results from the inability of ranges to grow across the boundary. When ranges expand at random, they are therefore more likely to grow in length (add area either above or below the current range) than in width (area can be added only opposite the boundary). In the truncation model, ranges have greater length because the portions beyond the hard boundary are being removed. Before the truncation, ranges on average grow to the same extent in both length and width. Once the boundary cuts off part of the width, the average length will be greater than the average width.

Range shape mostly has been ignored in previous null models of range distribution, largely because most of these models have been one-dimensional. Further investigation into the shape of real ranges near boundaries could yield useful information about the way ranges are determined at boundaries.

Conclusions

As in other arguments about null models in ecology (Gotelli 2001), it is not simple to determine what the proper assumptions should be for placement of species ranges in bounded domains. Different null models make different predictions about the effects of hard boundaries on species richness and other range characteristics. However, based on the flexible responses of real species ranges to changing conditions, I argue that a truncation model is more useful than others that assume that ranges are fixed. In any case, it is clear that not all geometric constraint models cause a mid-domain peak in richness. There does not seem to be a compelling argument for the use of null models based on fixed range sizes, and they should not have logical primacy in testing for spatial variation in species richness.

I suggest that the most parsimonious and productive approach for investigation of richness in bounded domains would be to return to a null model of unchanging species richness across the domain, including near domain boundaries. Any deviation from uniform richness is potentially informative and calls for further investigation. Rather than occupying the unique position of a null model, various forms of geometric constraint models could be considered within a more inclusive list of working hypotheses to explain patterns such as a decline in species richness near a domain boundary. It would be unfortunate if alternate hypotheses were dismissed without full exploration of other biologically interesting explanations.

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Figure 1 Three different approaches to null models that place ranges randomly in a bounded domain. If ranges are randomly placed without regard to a domain boundary (a), some ranges will cross the boundary (e.g. species 2). In the rejection model (b), any randomly generated range that crosses the boundary is eliminated from the simulation. Such rejection is done implicitly in models that assign a range size to a species and then allows the species to be placed only in locations that maintain the entire range within the domain. In the reshaping model (c), range shape is modified so that a specified range size is maintained, but the range is shifted to fall completely within the domain. For species 2, portions of the domain that would have fallen outside the boundary are eliminated (quadrats with X's) and a corresponding number of quadrats are added within the domain (black quadrats). In the truncation model (d), both range size and position are chosen independent of the domain boundary. Those portions of the range that fall outside the domain are eliminated (quadrats with X's) without replacement, so realized range size near domain boundaries could be smaller than the initially assigned value.

Figure 2 Species richness as a function of domain position in three null models. The curves shown are the means of 100 separate placements of 200 species, with varying mean range sizes. Standard error bars are too small to be visible around the symbols. Both the rejection and reshaping models produced declines in richness near the domain boundary, but the truncation model did not.

Figure 3 Range size as a function of domain position in three null models. Range size is expressed as a percent of the entire domain area. For each domain position, the mean range size is based on all ranges that overlap that position ('Stevens plot', see text). Curves show average range sizes after random placement of 10,000 species on the domain. In all three models, ranges sizes were chosen at random from a uniform distribution with mean range size of 20% of the domain, and a range from 10 to 30% of the total domain area.

Figure 4 Range shape as a function of range midpoint position in three null models. Shape is defined as range length (greatest extent of the range in the direction parallel to the domain boundary) divided by width (greatest extent of the range in the direction perpendicular to the domain boundary). Curves show average range shapes after random placement of 10,000 species on the domain; error bars are ± 1 SE. For most points the error bars are smaller than the symbols marking the means. In all three models, ranges sizes were chosen at random from a uniform distribution with mean range size of 20% of the domain, and a range from 10 to 30% of the total domain area Means are shown only for those domain positions with eight or more midpoints present. Since species number is much lower near the boundaries in the rejection and reshaping models (see fig. 2), there are not enough midpoints near the boundary to extend the curves to the domain boundary for these models.

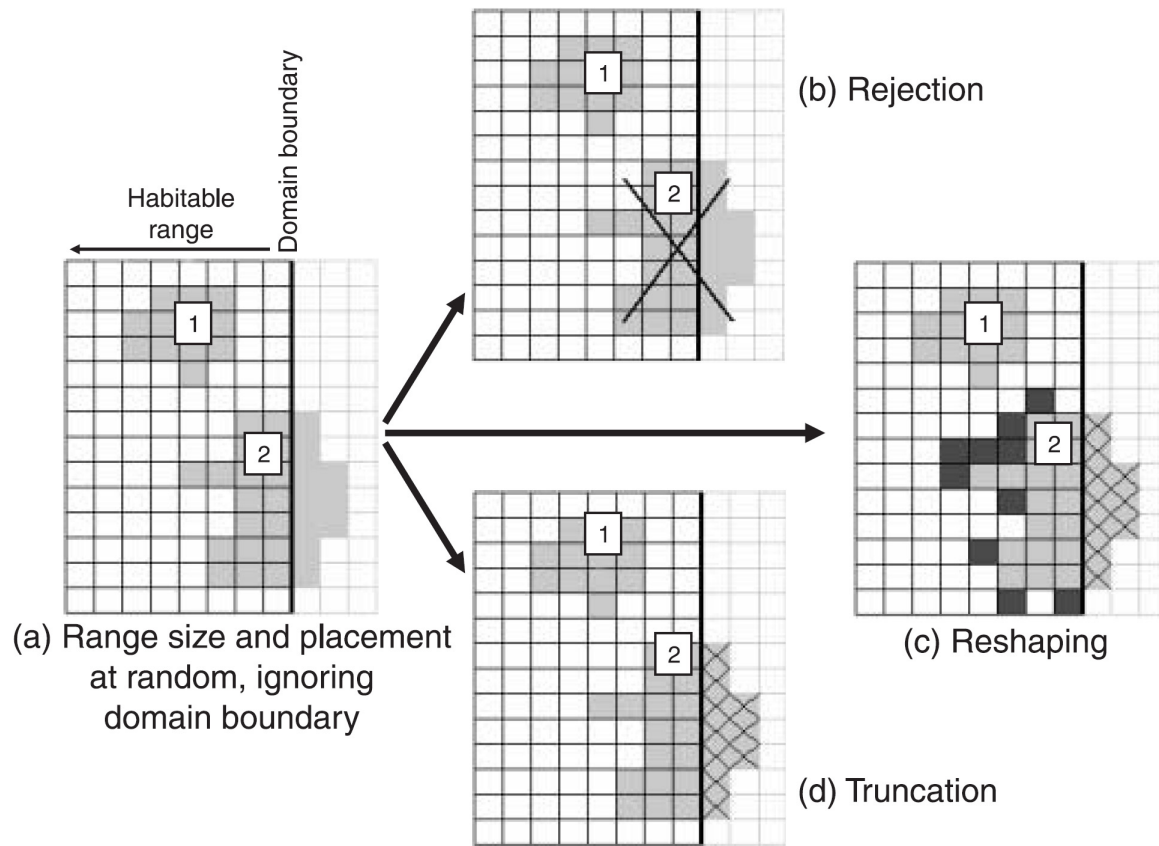


Figure 1

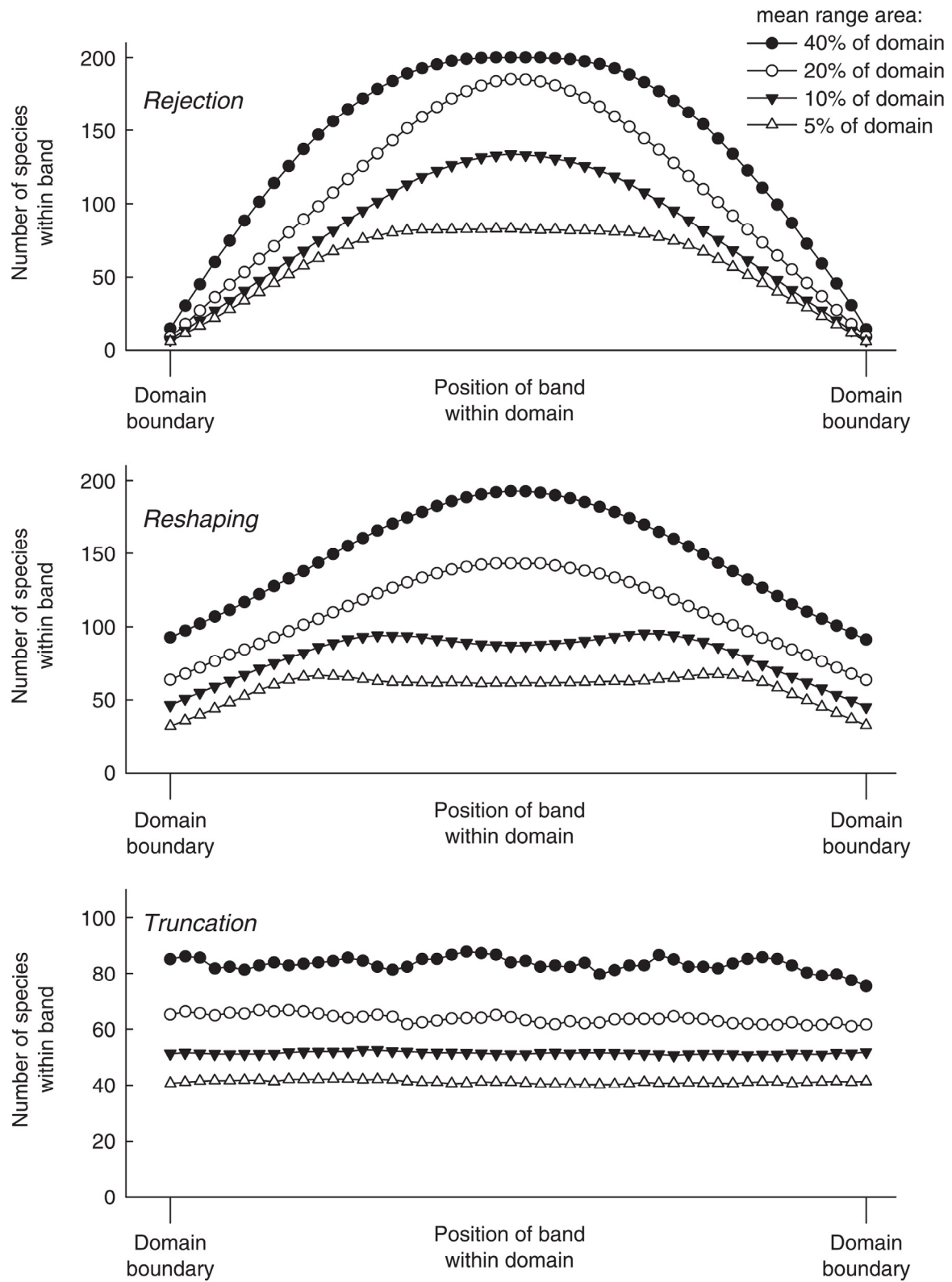


Figure 2

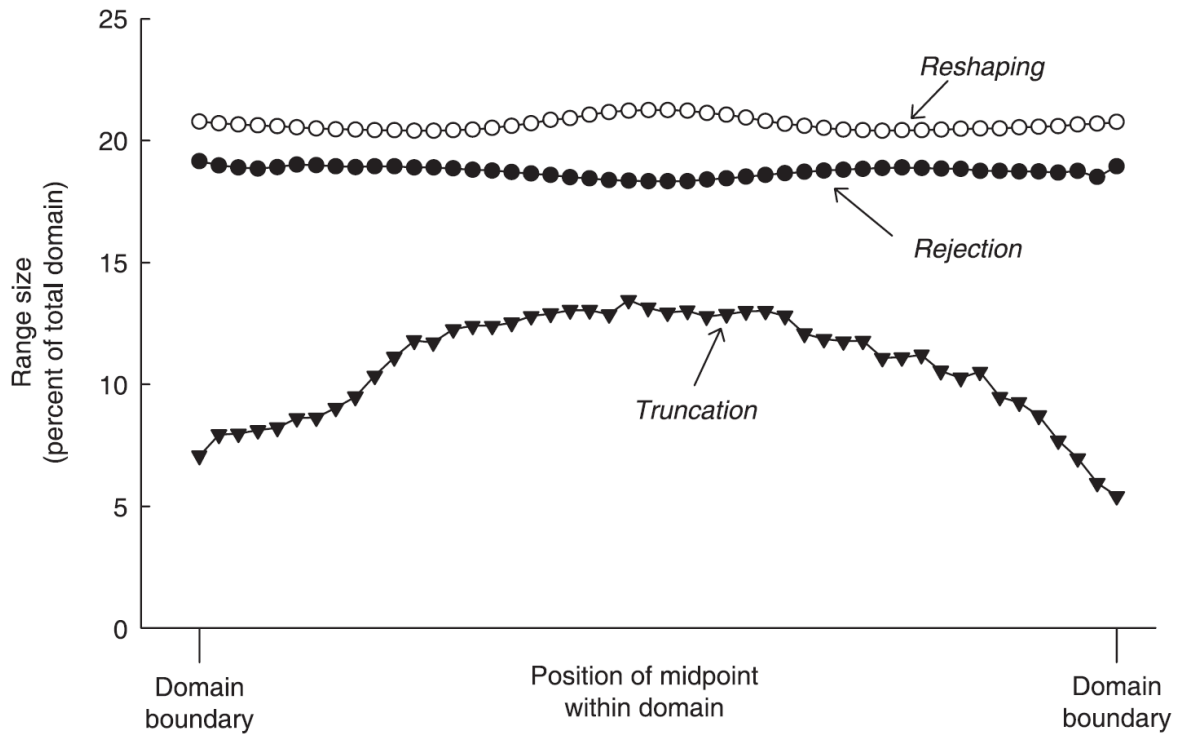


Figure 3

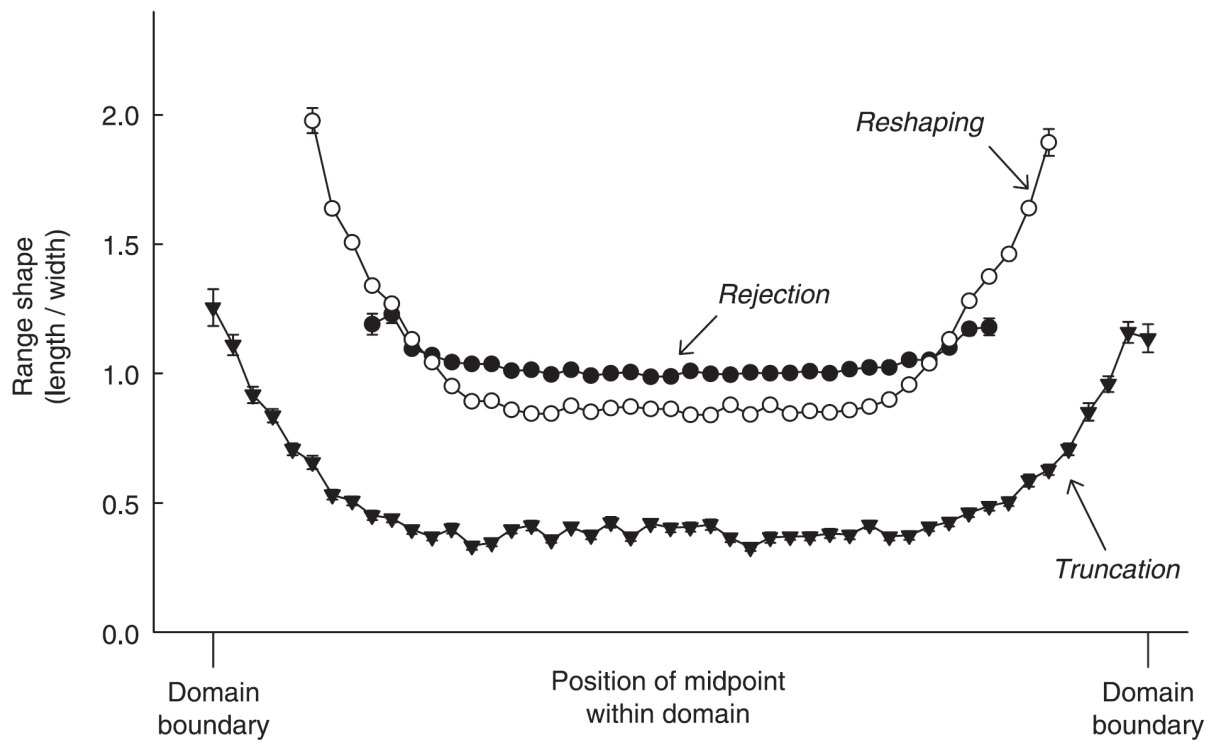


Figure 4

Chapter 2
Geometric constraint model
selection – an example with New World
birds and mammals

Abstract

Geometric constraint models (GCMs) of species distributions may be important tools for understanding macroecological patterns. However, there are currently a wide range of models in use, and few established criteria for selecting a model to use in a particular case. I propose a model selection procedure that uses multiple macroecological patterns to select the best-fitting GCM. I then demonstrate this method by comparing the fit of three GCMs to patterns of richness, range size and range shape of New World birds and mammals. Which GCM fit best depended on the average range size of the group in question, suggesting that the choice of which GCM to use can and should be context-dependent. I propose objective model selection criteria that offer a promising basis for making this choice.

Introduction

Species' distributions are subject to geographic boundaries, which may be due to climate, physical features or the distribution of other species. Certain boundaries, such as the edge of a continent or the elevational maximum of a mountain range, provide a hard constraint to the distribution of large numbers of species. These shared range constraints have consequences for the distribution of ranges within the habitable domain (Colwell and Lees 2000). Shared domain boundaries can produce non-uniform patterns of within-cell (α) diversity (Colwell and Hurtt 1994), between-cell turnover (β diversity, Koleff and Gaston 2001), range area (Koleff and Gaston 2001, Arita 2005, Sandel and McKone 2006) and range shape (Sandel and McKone 2006). Previous work has focused most heavily on patterns of α diversity, typically finding a peak in species richness in the middle of the habitable domain (Colwell and Lees 2000).

Domain boundaries can affect species distributions in a number of ways (Grytnes 2003). For example, species near a boundary may have small ranges, as the boundary eliminates areas that might otherwise be suitable habitat for them. Such small-ranging species may be at greater risk of extinction, producing a local decline in species richness near the domain boundary (Colwell and Hurtt 1994, Grytnes 2003). Similarly, while areas near the mid-domain may receive immigrants from all directions, locations near the domain boundary will typically not receive immigrants from beyond the boundary. To the extent that species richness is maintained and promoted by immigration, this will cause richness to decline near the boundary (Bokma et al. 2001, Grytnes 2003).

This suggests that large-scale analyses of species richness and other patterns may be incomplete without a consideration of how domain boundaries affect species distributions (Colwell and Lees 2000). Geometric constraint models (GCMs) are tools to assess and model this effect. GCMs may explicitly model the processes of speciation, range expansion or contraction and extinction that are thought to generate domain boundary effects (Bokma et al. 2001, Rangel and Diniz-Filho 2005a, 2005b, Rangel et al. 2007), or may represent these processes more abstractly (e.g. Colwell and Hurtt 1994, Jetz and Rahbek 2001, Sandel and McKone 2006). In either case, the goal of the exercise is to estimate the contribution of domain boundaries to patterns of species distribution, alone or in combination with other drivers of patterns.

GCMs are becoming widely applied, with the result that there are today a wide variety of GCMs in use (Bellwood et al. 2005). These models make a correspondingly diverse body of predictions (Bellwood et al. 2005, McClain and Etter 2005, McClain et al. 2007). Because of

this diversity, biological inference based on GCMs is sensitive to model choice. Despite the importance of model choice and the large number of models available, many studies use just one model to determine the contribution of geometric constraints. This may be due in part to a lack of published methods for choosing between multiple GCMs.

Model selection procedures have been slow to develop for GCMs, perhaps in part because they have traditionally been treated as null models. Most model selection procedures consider the fit of the model to data, but this is inappropriate in the case of null models; failure of a null model to fit data simply indicates that other processes not included in the null model are important (Colwell et al. 2004). As such, there is no way to use data to select one model over another, which makes model selection challenging (McClain et al. 2007). However, GCM predictions can also productively be thought of as candidate explanatory variables – to be tested in the same ways as other candidate variables (Currie and Kerr 2008). Under this framework, various hypotheses for the role of geometric constraints in driving any macroecological pattern can be tested against one another in the same way one would test hypotheses about the roles of various climatic factors, for example. If GCMs are viewed in this way, the fit of models to data becomes an appropriate basis upon which to compare models.

If we are to pursue this latter approach, a critical question is whether there is one most appropriate GCM to use in all situations, or whether the choice of GCM should be tailored to the domain, taxon and scale at hand. If there is one best GCM, the consideration of just one GCM in each study may be justified (though the use of different GCMs in different studies remains troubling). However, if GCM choice must be context-specific, then we need methods to make this choice rigorously and based on features of the data.

Selecting the most appropriate GCM provides improved inference about causes of macroecological patterns for at least two reasons. First, because GCM predictions can be combined with other predictors of patterns such as temperature and precipitation (Rahbek et al. 2007), the accurate assessment of the role of such predictors will depend on using an appropriate GCM. Second, the patterns predicted by the GCM itself may suggest particular biological processes (Grytnes 2003). For example, source-sink dynamics, range shifts due to environmental patterns and differential extinction of small-ranged species may have recognizable, distinct signatures in macroecological patterns, which may be revealed by fitting an appropriate GCM (Grytnes 2003).

In this paper, I propose and demonstrate a data-based method to select a GCM for use with a given data set. The method used here is to compare patterns of richness, range area and two measures of range shape for the group of interest to predictions of these patterns from multiple GCMs. Model performance is assessed for each parameter using a modified r^2 that combines information on the slope, intercept and scatter of the model-to-data fit (r^2_{ULR} ; Romdal et al. 2005). Information from multiple parameters is combined using principal components analysis, and a new selection criterion is used to score each model. The best performing model can then be used to generate an expected pattern of species richness and perform the various other functions of a GCM.

Two important features of the approach presented here are that it 1) is based entirely on the fit of models to empirical data and 2) uses multiple empirical patterns simultaneously to assess model fit. Basing model selection only on their fit to data produces at least two benefits. First, it provides an objective measurement of model performance, independent of debates over which GCM is most subjectively “reasonable” (Sandel and McKone 2006). While details of the selection procedure may be debated, the theoretical basis of each model need not be. Second, it

provides a common ground on which unlike models may be compared. As long as each model makes predictions for each pattern under consideration, the models can be assessed using this method. This is a substantial strength, as GCM models are becoming more and more dissimilar algorithmically (e.g. Bokma et al. 2001, Rangel and Diniz-Filho 2005a, 2005b, Storch et al. 2006, Rahbek et al. 2007), and are thus more difficult to compare.

The second important feature of this approach is the use of multiple patterns to judge model fit. Using multiple uncorrelated empirical patterns provides multiple independent assessments of model fit, and therefore produces a stronger set of selection criteria. This is important, as any given pattern may be spuriously correlated with a model prediction. For example, GCM predictions for species richness are often strongly collinear with other possible explanations (Currie and Kerr 2008). The probability that other features of species' ranges will also covary in the same way decreases as the number of independent patterns is considered. Thus, the probability of spuriously supporting a GCM decreases as more patterns are considered.

I demonstrate this method using three GCMs: the rejection, reshaping and truncation models of Sandel and McKone (2006). These are all 2-dimensional spreading dye models (Jetz and Rahbek 2001), but represent two extremes and an intermediate position in how ranges near the domain boundary are treated. I compare these predictions against real patterns of range size in terrestrial birds and mammals. I ask whether one model consistently outperforms the other two, or whether the best-performing model depends on the species group under consideration.

Methods

Range data

Range data for all terrestrial New World mammals and birds were obtained from the NatureServe database (Patterson et al. 2005, Ridgely et al. 2005). In total, the dataset included 1715 species of mammals and 3840 species of birds. The range map for each species was rasterized at 0.5 by 0.5 degree resolution. Species whose range did not overlap the midpoint of at least one cell were excluded from the analysis. Portions of ranges that occurred on islands that were not contiguous with the mainland at this resolution were ignored. Mammals and birds were treated separately.

For each species, I determined the total number of grid cells occupied by the species (range area), the ratio of the maximum north-south extent to the maximum east-west extent (shape1, the "shape" of Sandel and McKone 2006) and the ratio of the maximum northwest-southeast extent to the maximum northeast-southwest extent (shape2). Data from individual species were then combined by examining each grid cell in turn and counting cell species richness, then averaging the range area, shape1 and shape2 values for all species occurring in that cell. To improve normality, shape1 and shape2 values were log-transformed prior to analysis. Range area is presented in units of 0.5 x 0.5 degree cells occupied, while the range shape parameters are unitless log ratios.

As a result of counting each species in each cell where it occurs, species are not given equal weight. Large-ranging species will influence a large number of cells, such that patterns shown by small-ranging species may be difficult to detect if they are included in the same analysis as large-ranging species. In addition, the accuracy of a GCM model is expected to depend in part on the average range size considered (Dunn *et al.*, 2007). To examine the effect of range size on model fit and selection, I analyzed the entire group and each range size quartile separately.

Simulations

I used three approaches to randomly placing species ranges: the rejection, reshaping and truncation models discussed by Sandel and McKone (2006). All models use a spreading dye algorithm (Jetz and Rahbek 2001). Under this approach, generating a species' range begins by determining a range size and an initial grid cell. The range then expands iteratively, one square at a time, with equal probability to any square adjacent to the current range. This continues until the predetermined range size is reached. Range sizes were drawn without replacement from either the true range size frequency distribution (RSFD) for the group, or from a slight modification of it (see Truncation model details below). Using the empirical range size frequency maximizes the potential for a GCM to produce accurate fits to empirical patterns, and is common in GCM applications (e.g. Jetz and Rahbek 2001, Storch et al. 2006, Rahbek et al. 2007).

A simulation run consists of placing a randomly generated range for each species in the group. This produces a set of range maps that is comparable to the real set of range data for the group. These simulated range maps were then compiled in the same manner as the real data, and the same four maps were produced: species richness, area, shape1 and shape2. The data presented here are the averages of 50 replicate simulation runs. As with the real data, separate simulations were performed for the complete data set and each range size quartile for each group.

While the models all use the same basic range placement algorithm, they differ critically in how ranges that contact or overlap the domain boundary are treated.

Rejection model

The rejection model is a two-dimensional analog of Colwell and Hurtt's model 2 (1994). Under the rejection model, any range that grows beyond the domain boundary (in this case, the map of North and South America) is discarded, and a new starting point is selected. The rejection model preserves the input RSFD by continuing to select new starting points until a range of predetermined size is obtained. Thus, simulations under the rejection model simply used the real RSFD of each group as the input RSFD.

When applied to a two-dimensional domain with complex shape, the rejection model is unable to handle very large ranges. This is because the largest bird and mammal ranges are a sizable percentage of the total continental area. The probability of randomly producing a range of such large size that does not overlap the continental boundary is essentially zero. Because of this, only results for the first three range size quartiles are presented for the rejection model.

The rejection model has been shown to produce strong mid-domain peaks of species richness, little variation in range size with domain position, and relatively slight changes in range shape as the domain boundary is approached (Colwell and Hurtt 1994, Sandel and McKone, 2006).

Reshaping model

The reshaping model is very similar to that used by Jetz and Rahbek (2001). The reshaping model simply constrains ranges to stay within the domain by assigning expansion probabilities of zero to all grid squares that lie outside the domain. Like the rejection model, the RSFD output by the model matches the input. Therefore, real mammal and bird RSFDs were used.

The reshaping model produces moderately strong mid-domain peaks of species richness, invariant range size across the domain and strong changes in range shape near the domain boundary (Sandel and McKone 2006).

Truncation model

The truncation model is a two-dimensional analog of Colwell and Hurtt's model 1 (1994). It is the only model that is blind to domain boundaries while the range is initiated and grown. Only after the range has grown to its pre-determined size is the relationship of the range to the domain examined. If none of the range falls within the domain, then the model generates a new shape and starting location for that species until one does overlap the domain. Once a range is obtained that at least partially overlaps the domain, the portion of the range lying beyond the boundary is discarded, and the model proceeds to the next species.

Because it is possible for a range to begin off the domain and grow onto it, it is necessary for the area of possible starting locations to be quite large. For the purposes of these simulations, a buffer of 64 cells to each side of the map of the New World was sufficient.

The truncation model reduces range sizes by discarding the portion of ranges that extend beyond the domain boundary. To obtain an output RSFD that resembles the true RSFD for a group, it was necessary to modify the input RSFD. I generated output RSFDs for many possible transformations of the input RSFD. For both birds and mammals, I found that multiplying the input RSFD by a factor of five produced an output RSFD which satisfactorily matches the real, untransformed, RSFD (first, second, and third quartiles of the simulated RSFDs were all within 15% of the real RSFDs). For the simulations that considered each range size quartile separately, all ranges were placed, but those whose range size fell outside the span of ranges in the empirical range size quartile were discarded.

Range placement under the truncation model may be interpreted as the random assignment of a range of climatic conditions in which each species is able to persist, followed by the placement of that species on all land grid cells where those conditions exist. The truncation model produces no gradient in species richness, a strong decrease in range size near the domain boundaries and a moderate change in range shape near the boundary (Sandel and McKone, 2006).

Simulations and range analysis utilities were written in C++, and are available upon request from the author.

Assessing model fit

I assessed model fit by examining the regression of observed versus predicted values for each of species richness, range size, shape1 and shape2. The GCMs considered here make explicit predictions regarding these patterns. A perfect match of model to data should therefore produce a linear regression with slope one, intercept zero and r^2 of one. Model-to-data regressions differ from this ideal in various ways. This poses a problem for model selection, as it is possible that one model will have the slope closest to one, another an intercept closest to zero and the third the highest r^2 . It is therefore desirable to have a single criterion on which to base judgments of model fit that combine these three factors. Unity-line r^2 (r^2_{ULR} , Romdal et al. 2005) is such a parameter. r^2_{ULR} is similar to a traditional r^2 , except that, rather than calculating deviation from a fit regression line, it uses deviation from the one-to-one line. As such, it combines information on both the position of ordinary least squares (OLS) regression line relative to the ideal one-to-one line and scatter about that OLS line. If the OLS regression is the one-to-one line, $r^2_{ULR} = r^2_{OLS}$, otherwise $r^2_{ULR} < r^2_{OLS}$.

Each model considered here makes predictions for species richness, range size, and two measures of range shape. Ideally, these would provide four independent tests of the model. In practice, however, these range parameters are correlated in both empirical and simulated data. Accordingly, I used principal components analysis (PCA) to create new, uncorrelated axes. I performed PCAs on the four parameters of the empirical data for each species group, and then applied the same rotations to the model outputs for that species group (Table 3). This ensures that the four resulting empirical PCA axes for a species group are uncorrelated and that they are comparable to the simulated PCA axes for that group. Data for each parameter was z-transformed, to a mean of zero and standard deviation of one prior to PCA, to ensure equal weighting of the four components. I then calculated an r^2_{ULR} value for each PCA axis for each model-empirical comparison. Finally, in order to summarize the fit of a model to data across all parameters, I calculated a summary statistic, PC_{comb} , which is the average of the r^2_{ULR} for each PC axis, weighted by the fraction of the variance explained by that axis. This has the effect of combining information from all four patterns, but giving the most weight to the PC axes that explain the most variation. Thus, PC_{comb} provides a summary of model fit that incorporates information on the slope, intercept and scatter of four independent model-to-data comparisons.

The slope and intercept of the prediction-actual regression may be interesting in their own right. However, residuals of OLS regressions typically showed strong spatial autocorrelation, making OLS an unreliable method for estimating regression parameters. I used simultaneous autoregressive models (SAR) to obtain regression line estimates while accounting for the spatial structure of the data (Rahbek et al. 2007). SAR models were estimated using the SAM software package (Rangel et al. 2006). Because SAR estimation is computationally intensive, I randomly selected 1500 grid cells for analysis for each model to data comparison. SAR models produced residuals with reduced, but not entirely eliminated, spatial autocorrelation. To assess the significance of the regression r^2 values, I performed Dutilleul's (1993) degrees of freedom correction, which accounts for spatial nonindependence.

Results

The rejection model produced a strong mid-domain peak of species richness, the reshaping model a moderate peak, and the truncation model a uniform pattern of species richness (Figs. 1, 2). Under the first two models, the peak is not in the middle of the latitudinal extent of North and South America, as some one-dimensional analyses have found (e.g. Willig and Lyons 1998), but rather in the approximate geometric center of each continent (Figs. 1,2; see also Bokma and Monkkonen 2000). However, none of these patterns closely matched the empirical pattern. Model predictions fit empirical patterns of species richness poorly, with r^2_{ULR} scores typically less or much less than 0.1 (Table 1).

Predictions for range area were similarly poor. The truncation model and rejection model both predict a mid-domain maximum of range area, while the reshaping model predicts only a weak pattern of range area across the domain (Figs. 1,2). In no case did a model achieve an r^2_{ULR} score of 0.1 or more.

The rejection model predicts no pattern of range shape, while predictions of range shape for the truncation models and reshaping model are both more complex and more accurate. r^2_{ULR} values for shape1 and shape2 were quite high, particularly for large-ranging species (Table 1). Some features of the empirical pattern were not recreated by the models, however, such as the strong effect of the Andes on shape1.

The rejection model never had the highest PC_{comb} score (Table 2). The truncation model was preferred in six of the ten cases, while the reshaping model was supported in the remaining four. The truncation model outperformed the others when applied to small-ranging species, while the reshaping model tended to be preferred for groups of large-ranging species.

Unsurprisingly, identification of the best performing model would have been very different, were it based on just one of the patterns considered (Table 1). The rejection model had the highest r^2_{ULR} (though still quite low) for species richness in all cases where it was applied. Regarding predictions for range area, the truncation model was preferred for most bird groups, while the reshaping model was preferred for most mammals. And, in general, the reshaping model tended to be more accurate in its predictions for shape1, while the truncation model was generally preferred for shape2. Thus, combining information from all patterns together using PC_{comb} provides a qualitatively different, and more complete, assessment of model fit.

Discussion

Which model performed best depends on the species group in question. This supports the idea that GCM choice should be specific to the characteristics of the group to which the model will apply. If GCMs must be tailored to specific circumstances, then rigorous methods are needed to select a model in each case. Using multiple patterns to judge model fit, summarizing model fit using r^2_{ULR} , and combining fit to multiple patterns using PC_{comb} provide a means for making this selection. This relatively straightforward procedure will hopefully help to remove a barrier to considering multiple GCMs in one study, and will help ensure that the most appropriate of the available models are being used in each case.

To highlight the importance of selecting the most appropriate GCM, consider the difference in predictions for species richness between the reshaping and truncation model. The truncation model predicts no gradient of species richness across the domain, while the reshaping model predicts a mid-domain maximum. Clearly, the perceived role of geometric constraints in shaping species richness patterns depends critically on which of these GCMs is used. However, without some sort of model selection procedure, there is no way to know which GCM to apply to a particular species group.

It is likely that other models would fit patterns for these species groups better than any model I have considered. To know that such a model is superior, however, will require methods similar to those demonstrated here. Through repeated subsection of new models to these or similar selection criteria, we can discard poor models, develop more accurate models and, critically, begin to understand the circumstances under which one model will outperform another. The present paper represents some first steps in that direction.

Results from this study give some hints about what a superior model might look like. I chose three models to use here because they represent three clearly distinct points along one axis of variation in GCMs – that is, how ranges near the domain boundary are treated. As the reshaping model was generally superior for large-ranging species, while the truncation model was preferred for small-ranging species, a hybrid model might be optimal for all species. When determining expansion probabilities, the truncation model does not penalize grid cells for lying off the domain, while the reshaping model assigns all such cells a probability of zero. Adding a factor that depends on the range size of the species in question that would adjust this probability between zero and one could generate a hybrid model that would behave like the truncation model for small ranging species, and like the reshaping model for large ranging species. A strength of

this model comparison method is that it allows the comparison of any number of dissimilar models, by focusing only on the fit of model predictions to data.

Consistent with the results from previous studies (Dunn et al. 2007), there is a general pattern across all four parameters that each model performs the best when applied to large-ranging species. As suggested by others (Lees et al. 1999, Dunn et al. 2007), this may represent the increased importance of geometric constraints when the ratio of range size to domain size is high. This occurs because large-ranging species are more likely to encounter the domain boundary than are small-ranging species. However, another feature distinguishes patterns of large and small ranging species: the former have higher degrees of spatial autocorrelation. As such, patterns for large-ranging species have fewer truly independent data points, and are thus more likely to produce high r^2 values merely by chance (Lennon 2000).

Parameter Selection

The use of four parameters to assess model fit resulted in qualitatively different model selection, compared to any one parameter assessed alone. This supports the idea that considering more parameters improves model selection, and suggests that it may be beneficial to consider even more patterns in future analyses. For example, rather than calculating just the mean range area for all species occurring in a cell, it might be informative to consider other characteristics of the distribution of range sizes of species occurring in each cell. Variance, skew and kurtosis of such range size distributions for South American birds have been shown to vary substantially on the continental scale (Graves and Rahbek 2005). GCMs also make variable predictions for such characteristics of per-cell range size distributions (Arita 2005), and it might be desirable to have GCMs which can match such empirical patterns.

In this analysis, I gave equal *a priori* weighting to the different macroecological patterns. This is practical and reasonable when dealing with only four patterns, but as the number of patterns considered increases, each added parameter is more likely to be collinear with previous patterns, providing redundant assessments of model fit. Adding or removing redundant patterns causes model selection to become unstable by changing both axis loadings and the proportion of variance explained by each PCA axis. Thus, it is desirable to avoid using multiple strongly correlated patterns. One way to assess this is to examine the proportion of variance explained by each PCA axis. If some axes explain a very small proportion of the variance, for example < 0.01 , this suggests that one or more patterns are providing redundant information, and could be eliminated.

Comparison to Previous Results

This study differs from several previous studies that find high or moderate correspondence between GCM predictions and bird species richness patterns (Rahbek et al. 2007, Romdal et al. 2005). Two factors likely contribute to this difference. First, this study examined two-dimensional predictions of GCMs, unlike the study by Romdal and colleagues (2005). And unlike Rahbek and colleagues (2007), I analyze North and South America together. Both differences are likely to reduce the observed model fit, as GCMs commonly perform more poorly in two dimensions, (Zapata et al. 2003, Colwell et al. 2004, Kerr et al. 2006) and allowing North American species to be placed in South America and vice versa removes a constraint that would increase model fit. Analyzing model-to-data fit should be done in two dimensions when possible. Given the large number of species that cross any possible division of North and South America, it seems artificial to treat them as separate domains. Any possible separation of North

and South America will produce a large number of species which are present in both, but endemic to neither, domain. Thus, if the data are available, I argue that the entire land mass should be treated as a single domain.

These results suggest that domain boundaries may be relatively unimportant in shaping species richness patterns for small-ranging species, but are likely to be important for large-ranging species. Both the truncation and reshaping models predict non-uniform patterns of range size and shape, suggesting that boundaries are quite important in shaping these parameters across all range size classes. Boundaries act in concert with other drivers of macroecological patterns such as topographic features (which strongly affect range shape) and climate (which influences species richness). Recent work has made substantial progress in combining GCMs with other such drivers of patterns (Storch et al. 2006, Rahbek et al. 2007).

Suggestions

Different GCMs predict make distinct predictions for species richness and other patterns. For them to be useful, it is critical that investigators use the most appropriate model for the species, region and scale in consideration. Thus, future work along these lines should consider multiple candidate GCMs, and subject them to model selection criteria. The procedure used here is one method of making this selection.

Given enough studies that have performed this or similar model selection procedures, it will be interesting and informative to investigate which conditions lead to particular models being selected. These conditions will likely include both abiotic and biotic factors. Abiotic possibilities include grain size, domain area, location and dimensionality. Of the many possible biotic determinants, I have shown that range size affects model selection. What other biotic factors will determine which of the available GCMs perform best for a particular species group?

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Table 1 Fit of models to data. Each of the rejection (Rej.), reshaping (Resh.) and truncation (Trun.) models make predictions for patterns of diversity, range size and range shape. These predictions were compared to empirical patterns for New World terrestrial birds and mammals, divided into four range size quartiles (decreasing from Q4 to Q1). For each model to data comparison, the slope and intercept of the simultaneous autoregressive model are presented, as well as the r^2_{ulr} , a measure of model fit that combines slope, intercept and scatter. Dutilleul's (1993) method was used to estimate effective sample sizes for these models; significant model to data fit is indicated in bold. Limitations of the rejection model made predictions for the fourth range size quartile (and consequently the group as a whole) impossible.

Table 2 Results of regression on PCA axes. Empirical patterns of diversity, range size, shape1 and shape2 for each species group were decoupled using PCA, to produce four uncorrelated axes of variation. Model predictions for these parameters were subjected to the same rotation. Shown are the r^2_{ulr} values for each PC axis, as well as the overall PC_{comb} score for each model-data comparison. The best PC_{comb} score for each species group is highlighted. r^2_{ulr} values in bold indicate a significant correlation between the empirical data and model predictions for that PCA axis. In general, the reshaping model performed well for large-ranging species, while the truncation model performed best on small-ranging species.

Table 3 Loadings and variance explained for each of the four PCA axes for the empirical data for each species group.

Figure 1 Empirical patterns and rejection, reshaping and truncation model predictions for bird diversity, range size and both measures of range shape. The rejection model maps are based on simulations using the 75% of species with smallest ranges. Range size is in units of cells occupied, while range shape is a unitless log ratio. Both rejection and reshaping models produce mid-domain peaks of diversity, while the truncation model shows no such pattern. Fits of model to data were weak for diversity and range size, but the truncation and reshaping models captured much of the qualitative pattern of range shape.

Figure 2 Empirical patterns and model predictions for mammal diversity, range area, shape1 and shape2. Details and units are as figure 1.

Table 1

	Diversity			Area			Shape 1			Shape 2			
	Rej.	Resh.	Trun.	Rej.	Resh.	Trun.	Rej.	Resh.	Trun.	Rej.	Resh.	Trun.	
All Birds	Slope	0.478	5.452	---	-0.594	-0.156	---	1.444	1.213	---	0.97	0.687	
	Int.	52.4	-971.8	---	7029	4825	---	0.206	-0.154	---	0.146	0.194	
	r^2_{ULR}	0.036	0.038	---	0	0.014	---	0.6	0.475	---	0.145	0.19	
Q4 Birds	Slope	0.629	2.201	---	-0.021	-0.039	---	1.157	0.981	---	0.774	0.608	
	Int.	19.8	-160.8	---	7104	6718	---	0.045	-0.234	---	0.157	0.25	
	r^2_{ULR}	0.103	0.172	---	0.063	0.024	---	0.601	0.428	---	0.094	0.089	
Q3 Birds	Slope	0.011	0.018	0.065	-0.117	0.741	1.097	1.321	1.647	1.368	0.859	1.241	0.806
	Int.	22.9	11.2	2.4	748	199	-18	-0.225	-0.092	-0.355	0.231	0.131	0.117
	r^2_{ULR}	0.041	0.002	0.006	0.009	0.042	0.095	0.162	0.609	0.563	0.048	0.295	0.408
Q2 Birds	Slope	-1.292	-0.462	0.702	-0.069	0.837	1.102	0.554	2.598	1.601	0.446	1.999	1.031
	Int.	15.1	13.0	3.5	151	36	0	0.209	-0.007	-0.247	0.002	-0.205	-0.087
	r^2_{ULR}	0.068	0	0.02	0.002	0.016	0.046	0.016	0.381	0.442	0.01	0.341	0.459
Q1 Birds	Slope	-3.063	-0.632	0.114	0.075	0.101	0.278	0.202	1.779	1.4	0.162	1.575	1.081
	Int.	5.0	4.0	3.0	22.2	20.9	16.7	0.005	-0.073	-0.11	0.083	-0.082	-0.101
	r^2_{ULR}	0.011	0.001	0	0	0.001	0.01	0.005	0.211	0.316	0.005	0.226	0.408
All Mammals	Slope	---	0.364	0.281	---	-1.118	0.013	---	2.279	1.974	---	1.093	0.804
	Int.	---	29.1	-4.2	---	6274	3198	---	0.188	-0.341	---	0.185	0.166
	r^2_{ULR}	---	0.026	0.001	---	0.059	0.013	---	0.505	0.443	---	0.153	0.149
Q4 Mammals	Slope	---	0.228	1.891	---	-0.941	-0.078	---	1.917	1.793	---	0.847	0.66
	Int.	---	-7.3	-62.1	---	7466	4083	---	0.06	-0.367	---	0.224	0.204
	r^2_{ULR}	---	0.049	0.079	---	0.085	0.013	---	0.513	0.409	---	0.092	0.057
Q3 Mammals	Slope	-0.205	-0.434	0.319	0.247	0.646	1.022	1.686	2.599	1.819	-0.025	1.609	0.903
	Int.	7.9	10.7	3.0	285	71	-45	-0.501	-0.33	-0.497	0.171	0.111	0.076
	r^2_{ULR}	0.007	0.006	0.004	0.038	0.029	0.075	0.127	0.479	0.464	0.001	0.429	0.516
Q2 Mammals	Slope	-1.383	-1.215	1.089	-0.084	0.353	0.177	0.704	1.978	1.543	0.348	1.913	1.174
	Int.	4.6	5.0	1.1	75	46	57	0.132	0.034	0.007	0.128	0.032	0.031
	r^2_{ULR}	0.084	0.007	0.08	0.001	0.004	0.001	0.03	0.208	0.36	0.003	0.277	0.425
Q1 Mammals	Slope	-2.101	0.896	0.246	0.106	0.099	-0.044	0.1	0.409	0.561	0.318	0.639	0.619
	Int.	1.9	1.4	1.5	10.2	10.1	12.1	-0.046	-0.503	-0.066	-0.003	-0.605	-0.041
	r^2_{ULR}	0.012	0.001	0.002	0.006	0.002	0.001	0.002	0.006	0.083	0.015	0.029	0.154

Table 2

		PC1	PC2	PC3	PC4	PC _{comb}
All Birds	Rejection	---	---	---	---	---
	Reshape	0.396	0.16	0.043	0.027	0.285
	Truncation	0.393	0.179	0.04	0.035	0.288
Q4 Birds	Rejection	---	---	---	---	---
	Reshape	0.517	0.09	0.087	0.019	0.36
	Truncation	0.515	0.103	0.043	0.022	0.357
Q3 Birds	Rejection	0.006	0.066	0	0.021	0.023
	Reshape	0.263	0.334	0.297	0.075	0.262
	Truncation	0.197	0.386	0.312	0.008	0.243
Q2 Birds	Rejection	0	0.004	0.011	0.002	0.003
	Reshape	0.156	0.318	0.076	0.092	0.172
	Truncation	0.19	0.365	0.166	0.136	0.221
Q1 Birds	Rejection	0.002	0.001	0.041	0	0.011
	Reshape	0.053	0.088	0.129	0.045	0.08
	Truncation	0.086	0.149	0.204	0.09	0.133
All Mammals	Rejection	---	---	---	---	---
	Reshape	0.364	0.069	0.055	0.013	0.26
	Truncation	0.295	0.084	0.113	0.018	0.223
Q4 Mammals	Rejection	---	---	---	---	---
	Reshape	0.357	0.027	0.02	0.039	0.25
	Truncation	0.32	0.046	0.033	0.029	0.23
Q3 Mammals	Rejection	0.056	0.066	0.002	0	0.039
	Reshape	0.294	0.243	0.157	0.116	0.224
	Truncation	0.355	0.194	0.005	0.252	0.228
Q2 Mammals	Rejection	0.007	0.012	0	0.008	0.007
	Reshape	0.093	0.123	0.126	0.053	0.1
	Truncation	0.188	0.251	0.171	0.103	0.185
Q1 Mammals	Rejection	0.018	0.002	0.002	0.003	0.007
	Reshape	0.013	0.016	0.006	0.013	0.012
	Truncation	0.035	0.034	0.023	0.013	0.028

Table 3

		Diversity	Area	Shape1	Shape2	Variance
All Birds	PC1	0.531	-0.637	0.556	0.050	0.598
	PC2	0.257	0.066	-0.253	0.930	0.268
	PC3	-0.708	-0.034	0.605	0.363	0.124
	PC4	0.388	0.767	0.511	-0.023	0.010
Q4 Birds	PC1	0.557	-0.604	0.495	0.281	0.635
	PC2	0.159	0.198	-0.430	0.866	0.241
	PC3	-0.623	0.149	0.653	0.405	0.113
	PC4	0.526	0.757	0.379	-0.081	0.011
Q3 Birds	PC1	0.650	-0.492	0.514	-0.266	0.385
	PC2	-0.172	-0.379	0.299	0.859	0.264
	PC3	0.009	-0.700	-0.711	-0.060	0.206
	PC4	0.740	0.353	-0.374	0.434	0.145
Q2 Birds	PC1	0.558	-0.593	-0.008	0.580	0.391
	PC2	-0.229	-0.091	-0.962	0.115	0.256
	PC3	0.759	0.157	-0.264	-0.574	0.181
	PC4	0.244	0.785	-0.064	0.566	0.172
Q1 Birds	PC1	-0.579	0.524	-0.510	0.360	0.300
	PC2	0.514	0.387	0.310	0.700	0.269
	PC3	-0.296	0.577	0.653	-0.391	0.251
	PC4	-0.560	-0.492	0.466	0.477	0.181
All Mammals	PC1	0.463	-0.529	0.528	0.476	0.658
	PC2	-0.557	-0.469	0.469	-0.499	0.208
	PC3	-0.688	-0.018	-0.067	0.722	0.093
	PC4	-0.041	0.707	0.705	0.044	0.040
Q4 Mammals	PC1	0.458	-0.505	0.515	0.520	0.677
	PC2	-0.652	-0.478	0.470	-0.355	0.193
	PC3	-0.502	0.504	0.297	0.637	0.081
	PC4	-0.337	-0.513	-0.653	0.445	0.049
Q3 Mammals	PC1	0.531	-0.521	0.350	0.569	0.371
	PC2	-0.400	-0.462	-0.696	0.378	0.273
	PC3	0.642	0.468	-0.579	0.185	0.187
	PC4	-0.382	0.545	0.242	0.707	0.170
Q2 Mammals	PC1	0.646	-0.353	0.611	0.291	0.317
	PC2	-0.200	-0.623	0.199	-0.729	0.268
	PC3	0.122	0.697	0.507	-0.491	0.219
	PC4	0.726	0.025	-0.574	-0.377	0.197
Q1 Mammals	PC1	-0.624	0.535	0.413	-0.392	0.295
	PC2	-0.297	-0.546	-0.387	-0.681	0.267
	PC3	0.448	-0.322	0.750	-0.363	0.243
	PC4	0.567	0.559	-0.341	-0.500	0.195

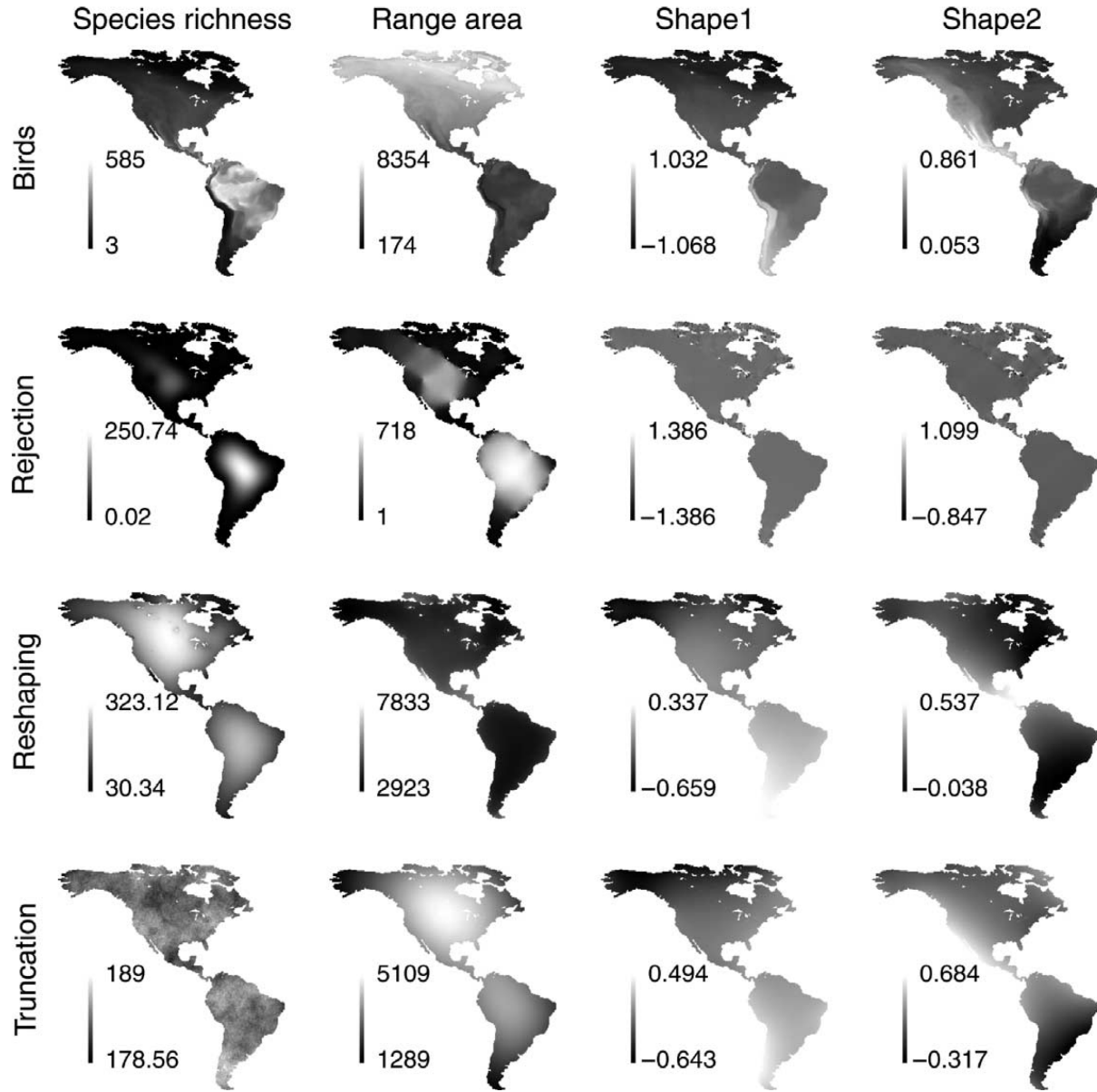


Figure 1

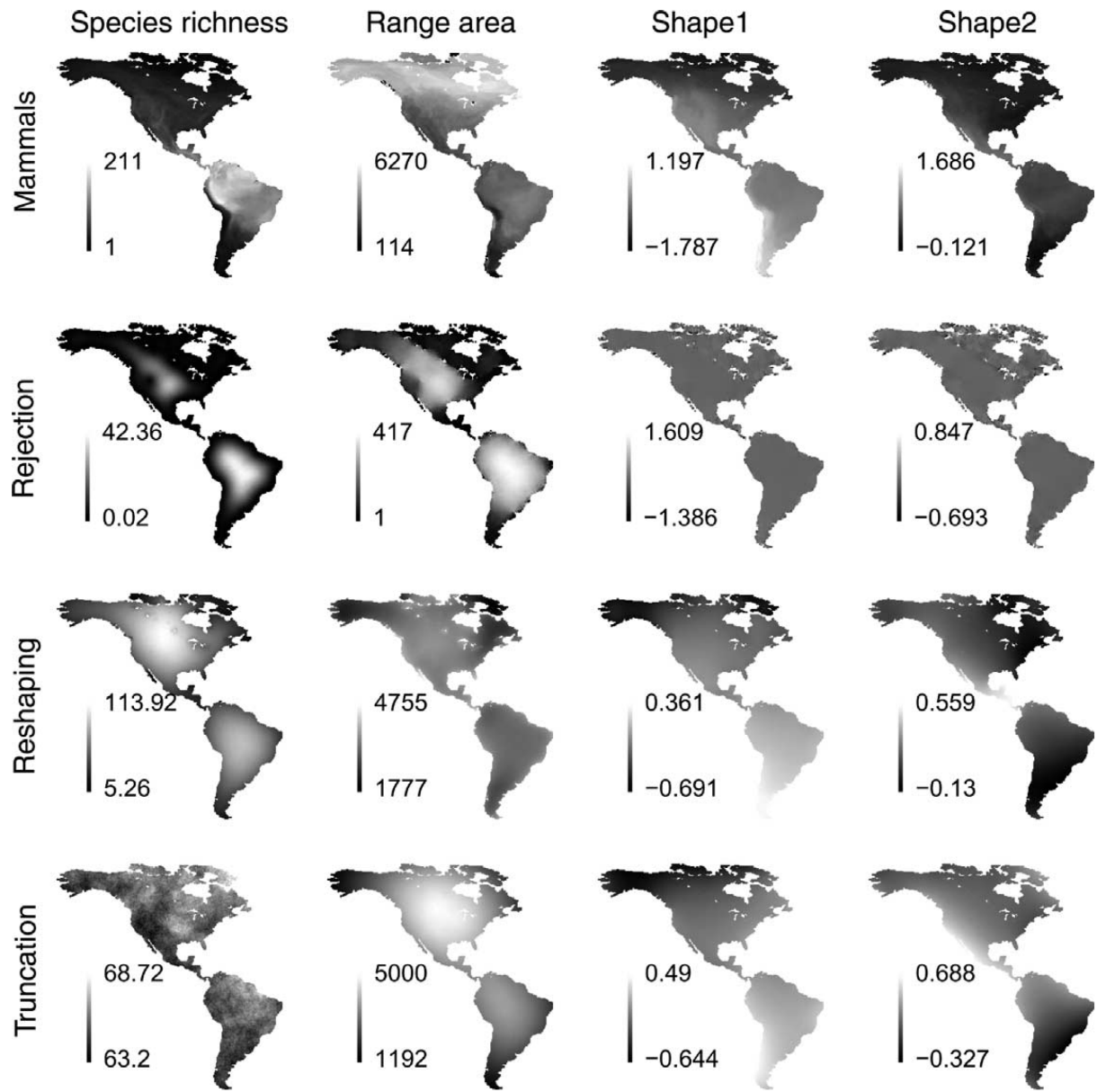


Figure 2

Chapter 3
Multi-scale ecological experiment
reveals mechanisms of scale-dependent
changes in diversity

Abstract

Species richness is a fundamental measure of biological diversity, important in both basic and applied ecology. A major challenge in understanding species richness patterns is that determinants of richness are often scale-dependent. Though rarely used in ecological experiments, the species-area relationship is a useful tool to summarize changes in species richness across multiple spatial scales. We assessed the changes in species-area relationships caused by manipulation of productivity and disturbance in coastal Californian grasslands. Responses of species richness were scale-dependent and complex, causing changes at any one scale to be difficult to interpret. However, both experimental treatments had consistent and interpretable effects on the species-area relationship. Reducing productivity increased the abundance of initially rare species and produced more aggregated spatial distributions of species. Disturbance tended to increase the abundance of already common species, and produced more even spatial distributions. These results suggest that debates regarding the productivity-richness and disturbance-richness relationships may be red herrings. To replace them, we suggest an increased focus on the effects of these factors on the species-area relationship.

Introduction

Understanding the causes of variation in species richness is one of the central enterprises of community ecology. It is becoming increasingly clear that this understanding will depend heavily on awareness of how spatial scale influences richness patterns (Wiens 1989, Levin 1992, Mittelbach et al. 2001, Whittaker et al. 2001, Sandel and Smith 2009). Different factors are important in determining species richness at different spatial scales (Ricklefs 1987, Huston 1999, Willis and Whittaker 2002) while particular factors can have different effects depending on scale (e.g. Olff and 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 and Schneider 2008, Sandel and 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) allows improved detection of subtle treatment effects, 2) bridges gaps between studies, possibly explaining discrepancies between them, and 3) improves mechanistic interpretations of treatment effects (Sandel and Smith 2009). The species-area relationship (SAR) is a useful tool to summarize treatment effects across multiple scales in ecological experiments. For example, species-area relationships (SARs) for control and treatment plots for some experimental manipulation might cross (fig. 1A,B). In this case, the treatment will be perceived as increasing, decreasing or not changing richness, depending on the scale of observation. 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 and Smith 2009).

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. In

both cases, results can appear statistically as interactions between treatment factors and spatial scale, or as a change in a cross-scale metric such as the SAR slope. Thus, examining richness responses across multiple scales allows a more precise understanding of treatment effects.

Interpreting changes in SAR

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 and 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 and Legendre 2002). Abundant and evenly-distributed species will tend to influence the SAR across the entire scale range more than rare or clumped species. It is possible to imagine various ways in which these three factors might respond independently or in concert to a particular experimental treatment, thereby altering the shape of the SAR in complex ways.

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 and D'Antonio 1999, Chesson et al. 2005). Scale-dependence also provides a potential general explanation for mismatches between experimental results and between experiments and observational studies, such that considering it explicitly may yield improved generalization regarding the factors that control species richness (Sandel and Smith 2009).

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 (see Allcock and Hik 2003, Crawley et al. 2005, de Bello et al. 2007).

Species richness generally increases with increasing productivity at large spatial scales (Francis and Currie 2003, Hawkins et al. 2003), but may be unimodal or negative at smaller spatial scales (Mittelbach et al. 2001, Chase and Leibold 2002, Harrison et al. 2006). 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 differences in experimental details is unclear, but these conflicting results certainly suggest that different processes appear to be important at different spatial scales. One explanation for this is the decoupling of α (within-plot) and β (between-plot) components of diversity in response to productivity (Chase and 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).

Species richness at any particular spatial scale may be maximized under intermediate disturbance intensity and frequency (Connell 1978, Sousa 1979), but a major disturbance at one sampling 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 (Hamer and Hill 2000, Mackey and Currie 2001, Kaiser 2003, Tylianakis et al. 2006). Multi-scale studies of tropical lepidopterans have shown that their response to disturbance varies with sampling scale, typically increasing with disturbance at small scales and decreasing at larger scales (Hamer and 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 species-area relationship. Disturbance-richness relationships at any particular single scale may be idiosyncratic and determined in large part by the relatively arbitrary choice of sampling scale.

A complete understanding of the relationship of richness to productivity and disturbance appears to require understanding of both α and β components of diversity. The SAR is a particularly useful tool to generalize from these components, as its use does not require the often arbitrary distinction of within- and between-plot scales, instead treating spatial scale as a continuous variable. Thus, we suggest that an increased focus on how disturbance and productivity affect SARs could be very useful.

In this paper, we ask whether the response of vascular plant species richness to experimental manipulations of productivity (via reverse fertilization) and disturbance (mowing) are scale-dependent. We use SARs to summarize treatment effects, and examine causes of changes in the SAR over four years and at two coastal grassland sites in California. In so doing, we demonstrate the above three benefits of multi-scale sampling in ecological experiments. We hypothesized that disturbance would consistently decrease the slope of the SAR, but that responses at any one sampling scale would be variable. As fertilization has been shown to lead to decreased α and increased β diversity, we hypothesized that reducing productivity might decrease SAR slope, while likely increasing richness at small spatial scales (fig. 1C,D)

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, 20 m a.s.l.) is a private reserve owned by Audubon Canyon Ranch. The Point Reyes site was located at Pierce Point Ranch, in the Point Reyes National Seashore (38 11' N, 122 57' W, 100 m a.s.l.). Both sites are dominated by exotic grasses, most notably *Bromus diandrus*, *Vulpia myuros*, *Holcus lanatus* and *Lolium perenne* (Hickman 1993). Native species are present but at very low abundances at both sites. These include *Bromus carinatus*, *Eschscholzia californica* and, to a lesser extent, *Hordeum brachyantherum* and *Danthonia californica* among others. Both sites have been free from livestock grazing for at least 35 years, 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 year, concentrated in the winter months. 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 rainy season (PRISM group 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* and *Baccharis pilularis* shrubs, which are abundant at both sites. Plots were 5 x 5 m at Point Reyes, and 4 x 4 m at Tom's Point, due to space limitations.

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 nitrogen becomes immobilized in microbial biomass, making it temporarily unavailable to plants (Wilson and Gerry 1995, Blumenthal et al. 2003, Corbin and D'Antonio 2004). Carbon was added in the spring and fall of each year as sucrose at 450 g/m², except the initial treatment which was 170 g sucrose/m² and 360 g sawdust/m². 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 approximately 10 cm. Following mowing, we removed all clippings from the plots. Mowing and reverse fertilization reduced end-of-season standing crop to similar degrees, ranging from 20-40%, and reverse fertilization reduced N mineralization rates by nearly 90% two weeks after sugar application (Chapter 4).

Sampling

We surveyed the plant assemblage in each plot between late May and early July in 2006, 2007, 2008 and 2009. The sampling unit was a 2 x 2 m plot arrayed in the middle of each treatment plot. This unit was gridded into sixteen 50 x 50 cm cells, each of which contained a 25 x 25 cm subplot, which in turn contained a 12.5 x 12.5 cm subplot. During each sampling year, we identified all vascular plant species rooted in each cell and subplot. This design allows 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 m² to 4 m².

Analysis

We summarized the spatial pattern of species richness for each plot by determining the slope and elevation of the SAR for that plot. The slope was calculated by taking the mean species richness at each scale, and regressing log(mean richness) against log(area). The elevation was defined as the mean species richness at the smallest sampling scale (0.016 m²). We tested for treatment effects using repeated-measures ANOVA, with treatment and site as fixed effects, and plot SAR slopes or elevations measured repeatedly across multiple years.

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. We call this the conditional occurrence probability (COP) for a species. The COP 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 controlling for differences in species' abundances. 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 x 50 cm subplot and four species occurred within a 25 x 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 species' mean COP for a specific scale transition across all plots 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), which is the mean difference between observed and expected community-wide COPs across all subplots within a plot (fig. 2). 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 m² scales, and between the 0.063 and 0.016 m² scales.

We then asked whether control plot occupancy rate predicts the response of species 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 x 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% cutoff. 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

SARs had a mean slope (z-value) of 0.259, which closely matches other small-scale SARs (Rosenzweig 1995, Drakare et al. 2006). SARs were well fairly linear in log-log space (average $r^2 = 0.979$), though most did show some downward curvature, as commonly found for SARs in this scale range (figs. 3, 4, Rosenzweig 1995, Carey et al. 2006).

In some cases, the average SAR for treatment plots crossed that for control plots (figs. 5, 6). In these cases the effect of reverse fertilization and disturbance depends qualitatively on spatial scale. The slope of the SAR responded strongly to the treatments (Table 1, fig. 7). At both sites, reverse fertilization increased SAR slope, relative to the control. Disturbance tended to reduce slopes, relative to the control, especially at Tom's Point. Disturbance also increased SAR elevation (Table 2, fig. 8), while reverse fertilization tended to reduce it, especially at Tom's Point.

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. 8). In contrast, disturbance differentially benefited common species, with no effect on rare species ($F_{1,280} = 11.01$, $P = 0.0010$, fig. 10).

Considering the CEI based on occurrence probabilities at 0.063 m², conditional upon occurrence at 0.25 m², disturbance tended to increase evenness of species distributions, leading

to more homogenous plots ($F_{2,90} = 7.042$, $P = 0.0014$), though responses varied among years (Treatment by Year interaction $F_{6,270} = 2.737$, $P = 0.0134$, fig. 11). 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 fertilization increased aggregation ($F_{2,90} = 3.636$, $P = 0.0303$, fig. 12).

Discussion

Disturbance and productivity manipulations altered the slope of the species-area relationships at these sites. Disturbance tended to decrease the slope of the SAR, while reducing productivity tended to increase it. Therefore, for both treatments, the magnitude of the treatment effect on species richness depends on the spatial scale of observation. Furthermore, reverse fertilization caused reductions of richness at small scales and increases in richness at larger scales in some cases. Thus, the response of richness to productivity can also be qualitatively scale-dependent.

Interpretation of treatment effects

Productivity

Differences in observational scale may explain variable responses of richness to productivity among studies (Mittelbach 2001). Increasing productivity may decrease richness at small spatial scales (due possibly to competitive exclusion) but increase it at larger scales (due to increases in β diversity, Chase and Leibold 2002, 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. That is, reduced productivity often reduced species richness in small plots, but increased dissimilarity among small plots produced increases in richness at larger scales, leading to steeper SAR slopes, exactly as has been proposed 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 $>400 \text{ g ANPP/m}^2/\text{year}$, fertilization tended to decrease β diversity. The Tom's Point and Point Reyes sites typically produce about $600 \text{ g ANPP/m}^2/\text{year}$, so it is perhaps not surprising that we saw an increase in β following a decrease in productivity.

This suggests that a complete understanding of the productivity-diversity relationship may rely on separate understanding of α and β diversity patterns. The species-area relationship 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 response of the SAR to productivity should become the focus of increased research attention.

The response of the SAR to reverse fertilization in this study has a clear interpretation, consistent with theoretical expectations. Reducing productivity reduced the abundance of very abundant species (see also Sandel and Corbin 2010), allowing uncommon species to colonize these plots. This produced an increase in richness at the 4 m^2 scale. However, two factors prevented this increase from being seen at all spatial scales. First, species distributions became

more aggregated, leading to steeper SAR slopes (which corresponds with higher β diversity). As well, the reduced abundance of common species (and corresponding increase in bare ground) reduced species richness at the smallest spatial scales.

Disturbance

The reduction of the SAR slope with increased disturbance is consistent with previous observational results at larger scales for lepidopterans (Hamer and Hill 2000, Hill and Hamer 2004, Dumbrell et al. 2008), but opposite to patterns observed for birds (Hill and 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, leading to reduced large-scale richness (Dumbrell et al. 2008). This is generally consistent with the mechanisms detected in this study. Richness at the smallest scale did increase with disturbance, but 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 and Hill 2000).

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. Hence, we suggest that asking how species richness responds to certain factors is unlikely to be as informative as asking how the species-area relationship responds (Pastor et al. 1996, Weiher 1999).

Above, we described three benefits of multi-scale sampling in ecological experiments. It improves 1) our ability to detect responses, 2) generality, by allowing detection of scale-dependent responses, and 3) mechanistic explanations of treatment responses. We have demonstrated all three of these benefits in this study. Examining treatment effects at multiple spatial scales not only allowed a more comprehensive interpretation of changes in species richness, but also revealed changes that might not have even been observed at the commonly used 1 m² plot. Had we analyzed only richness responses at this scale, we would have detected no significant treatment effects (Repeated Measures ANOVA, $F_{2,90} = 1.340$, $P = 0.2671$). Focusing on the SAR, rather than on richness at a single scale, also revealed a general pattern that would not have been detectable otherwise. At both sites, reverse fertilization increased the slope of the SAR, but often had contradictory effects on single-scale richness between the two sites.

Much research (Waide et al. 1999, Mittelbach et al. 2001, Mackey and Currie 2001) has disagreed on the form of the productivity-diversity and disturbance-diversity relationships. One likely explanation for this is that studies are performed at different spatial scales (Chase and 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 the mechanistic basis for changes in species richness across scales. Coordinated changes in species abundance distributions and spatial patterns can cause treatment effects to be scale-dependent in ecological experiments.

Conclusion

In general, responses of species richness to experimental treatments have the capacity to be more complex than simply increasing or decreasing. Measuring species richness across multiple spatial scales and examining changes in the SAR allow complex responses to be described. In this study, we have demonstrated that altering productivity and disturbance can have both quantitatively and qualitatively scale-dependent effects on species richness. This is in accord with previous work that suggests that the productivity-diversity relationship is scale-dependent, though the observed changes in beta diversity differed from those of some previous work.

Obtaining a scale-dependent result in this case demonstrates the utility of multi-scale sampling in ecological experiments. It provides a more complete description of experimental responses, suggests more mechanistic understanding of the basis for the response (in this case, shifts in the SAD), and promises to provide a framework for unifying disagreeing experimental results.

That a given restoration treatment can have scale-dependent effects on species richness has important consequences for land managers as well. Our results suggest that, in some cases, management to maintain diversity must also designate the relevant spatial scale, as a given treatment might have positive consequences at one scale and negative consequences at another. Thus, it may be necessary to prioritize either large or small scale richness as the conservation goal.

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Table 1: ANOVA table for repeated measures ANOVA, testing the effect of treatment on species-area relationship slope.

	DoF	MSE	F	P
Site	1	0.1417	56.96	< 0.00001
Treatment	2	0.0248	9.982	0.00012
S x T	2	0.0007	0.295	0.74
Residuals	90	0.0025		
Year	3	0.0668	87.94	< 0.00001
S x Y	3	0.0056	7.389	0.00008
Y x T	6	0.0054	7.084	< 0.00001
S x Y x T	6	0.0012	1.518	0.17
Residuals	270	0.0007		

Table 2: ANOVA table for repeated measures ANOVA, testing the effect of treatment on species-area relationship elevation.

	DoF	MSE	F	P
Site	1	185.3	167.1	< 0.00001
Treatment	2	12.48	11.26	0.00004
S x T	2	1.411	1.272	0.2852
Residuals	90	1.109		
Year	3	9.450	33.76	< 0.00001
S x Y	3	6.146	21.96	< 0.00001
Y x T	6	1.294	4.624	0.00017
S x Y x T	6	0.788	2.817	0.01125
Residuals	270	0.0007		

Figure 1 Examples of species-area relationships in an experimental context. Treatment and control SARs may cross (A), producing qualitatively scale-dependent results. Controlling for the effect of scale on richness in control plots (B) by subtracting the control mean richness at each scale from control and treatment richness values reveals treatment effects more clearly. Disturbance may decrease the slope of the SAR (C), but could have variable effects on SAR intercept, while reducing productivity (D) is expected to increase SAR intercept and reduce SAR slope.

Figure 2 Illustration of CEI calculation method. First, a mean conditional occurrence probability (COP) is calculated for each species (A, B and so on). This probability is defined as the probability that a species that occurs in a certain plot will also occur in some defined subset of that plot. Abundant or evenly dispersed species will tend to have high COP values (like species B). With COP values for each species, it is possible to calculate, for a given plot with certain species present, the expected community-mean COP value. The expected value takes into account each species' tendency to aggregate or be evenly distributed. Thus, comparing the observed community-mean COP value to this expected value gives an estimate of the community-wide evenness, relative to that expected, controlling for interspecific differences.

Figure 3 Species-area relationships at Point Reyes, across four years and three experimental treatments. Note the log scale of axes. The SARs were nearly linear, but showed slight downward curvature.

Figure 4 Species-area relationships at Tom's Point, across four years and three experimental treatments. Note the log scale of axes. The SARs, especially in the later years of the experiment were distinctly concave-down.

Figure 5 Species-area relationships at Point Reyes, standardized to the control mean at each plot size. These are the same data as fig. 1, but removing the effect of scale on species richness allows treatment affects to appear more clearly. 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 increased it at larger scales.

Figure 6 Species-area relationships at Tom's Point, standardized to the control mean at each plot size. These are the same data as fig. 2, but removing the effect of scale on species richness allows treatment affects to appear more clearly. 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.

Figure 7 Responses of species-area relationship slopes to experimental treatments. At both Tom's Point and Point Reyes, reverse fertilization increased the SAR slope in the last three years of the study, while disturbance decreased it, most strongly at Tom's Point.

Figure 8 Responses of species-area relationship elevations to experimental treatments. Disturbance typically increased SAR elevation, while reverse fertilization tended to decrease elevation.

Figure 9 Differential responses of rare and common species to reverse fertilization. Rare species increased in response to the treatment, while common species showed marked decreases, except at Point Reyes in 2008.

Figure 10 Differential responses of rare and common species to disturbance. Rare species showed no change in abundance with disturbance, but common species became even more common.

Figure 11 Changes in spatial evenness of species' distributions, considering the 0.063 m^2 occurrence probabilities, conditional upon occurrence at the 0.25 m^2 scale. Controlling for intraspecific 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.

Figure 12 Changes in spatial evenness of species' distributions, considering the 0.016 m^2 occurrence probabilities, conditional upon occurrence at the 0.063 m^2 scale. Controlling for intraspecific variation in abundance and tendency to aggregate (see text), species distributions, on average, became more aggregated in reverse fertilization plots.

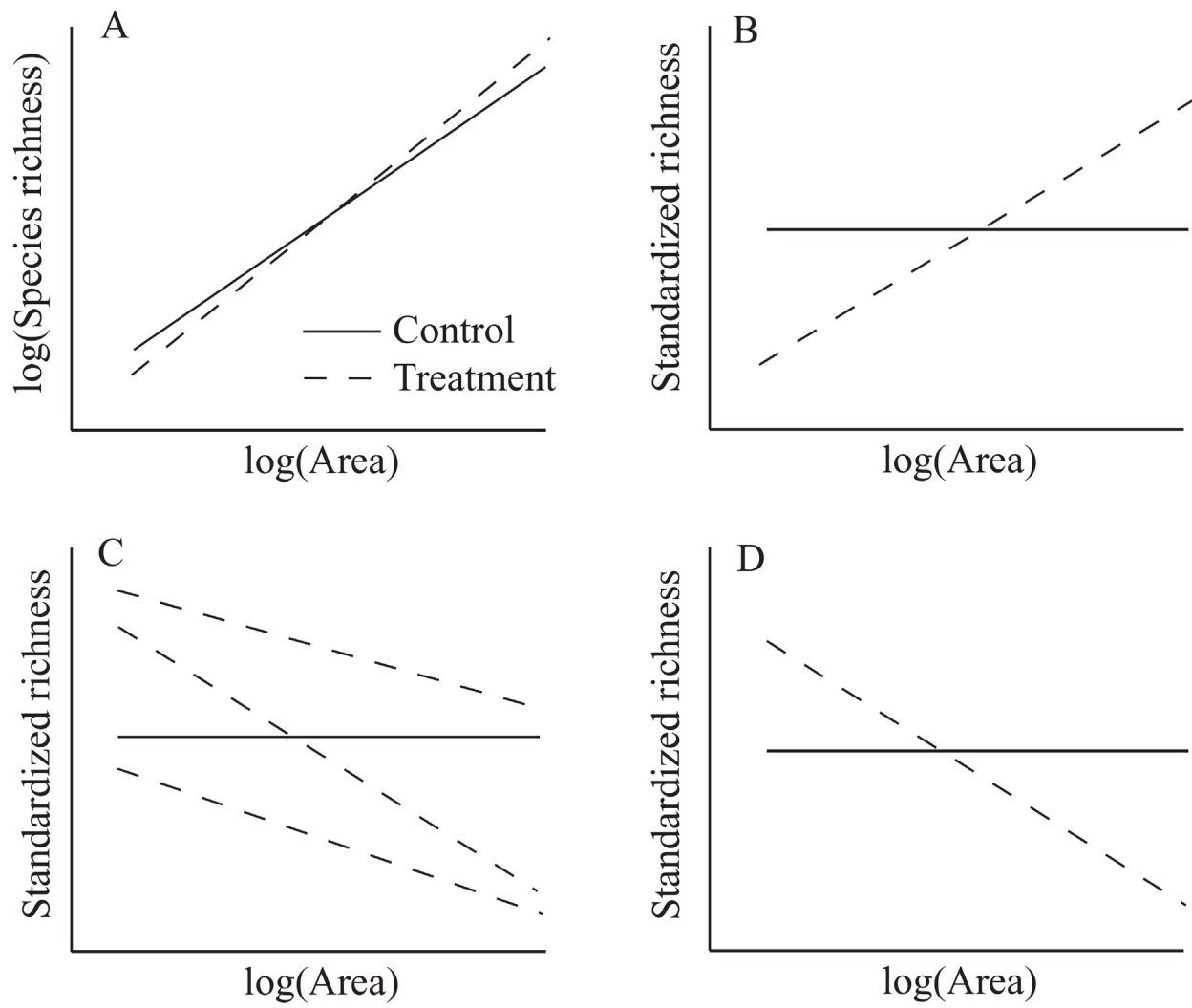
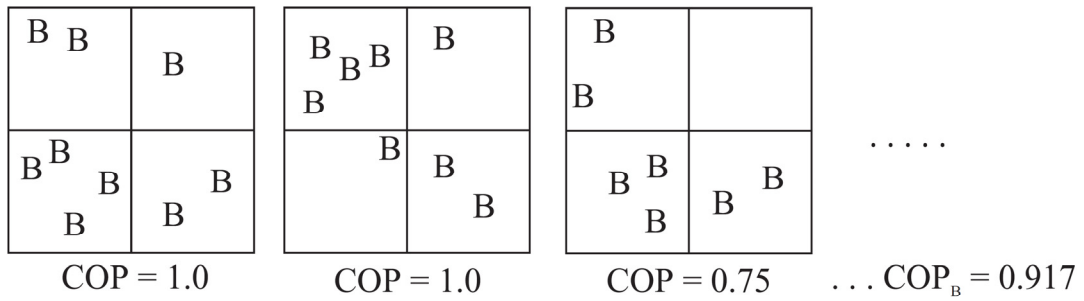
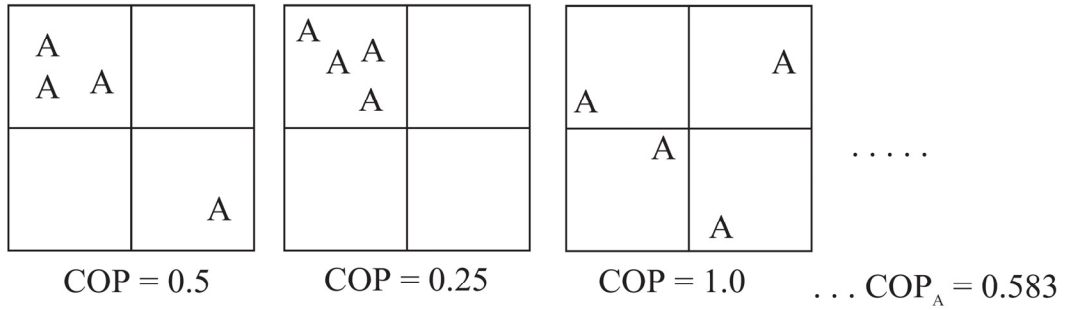


Figure 1



A A	B B
A	B
B	B

Expected Community COP = $(0.583 + 0.917)/2$
 $= 0.75$

Observed Community COP = $(0.5 + 0.75)/2$
 $= 0.625$

Community Evenness Index = $0.625 - 0.75$
 $= -0.125$

Figure 2

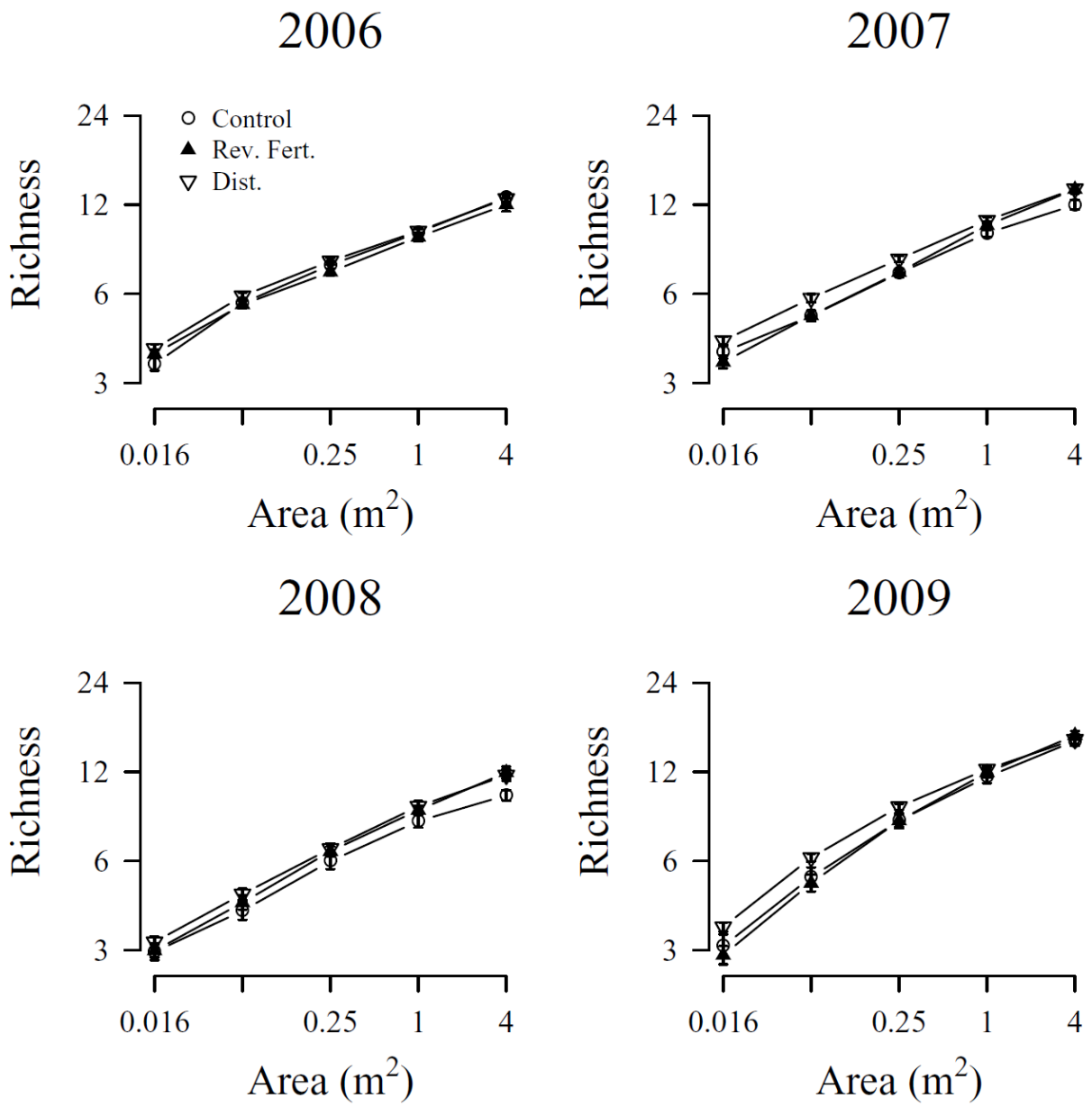


Figure 3

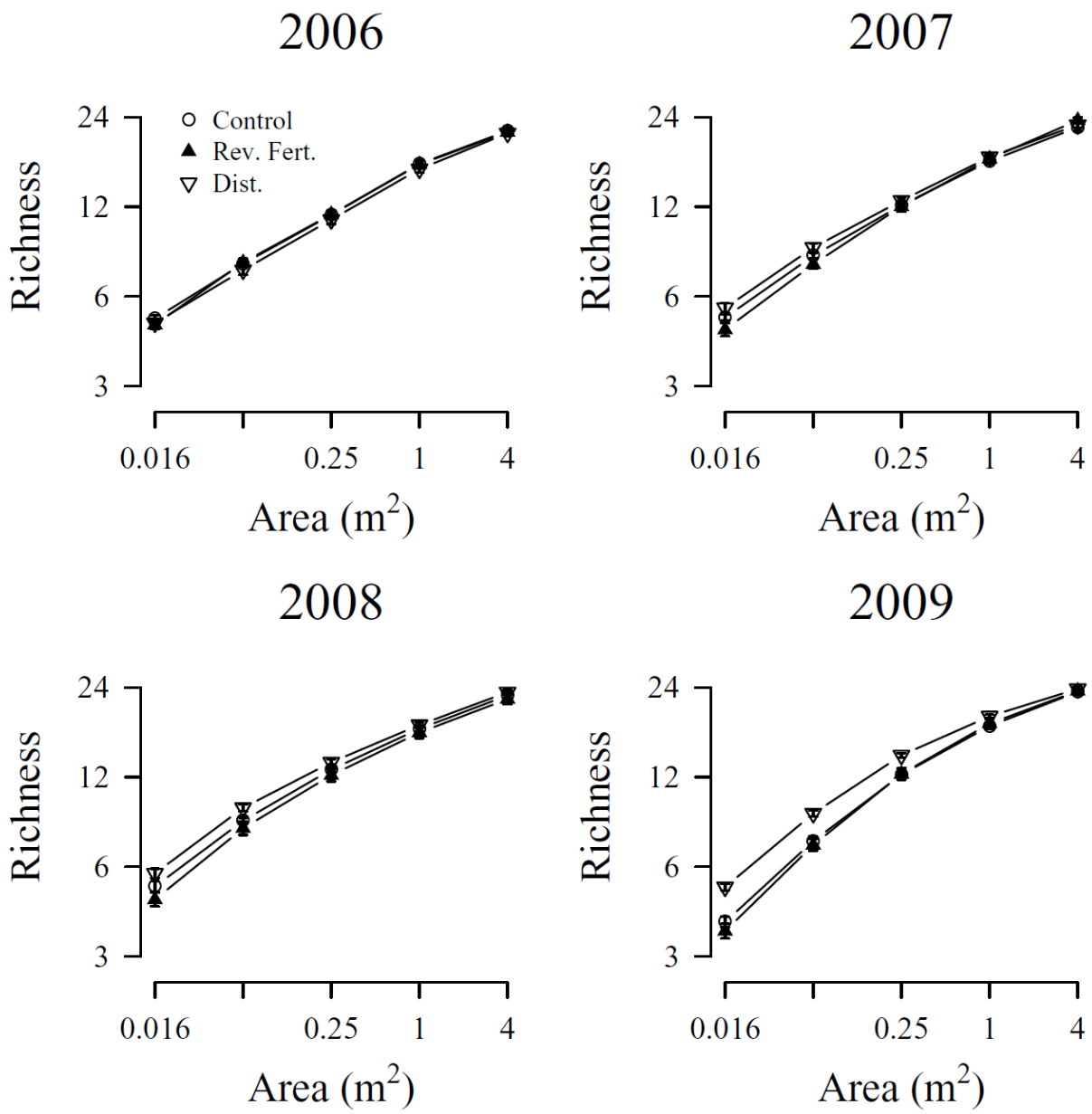


Figure 4

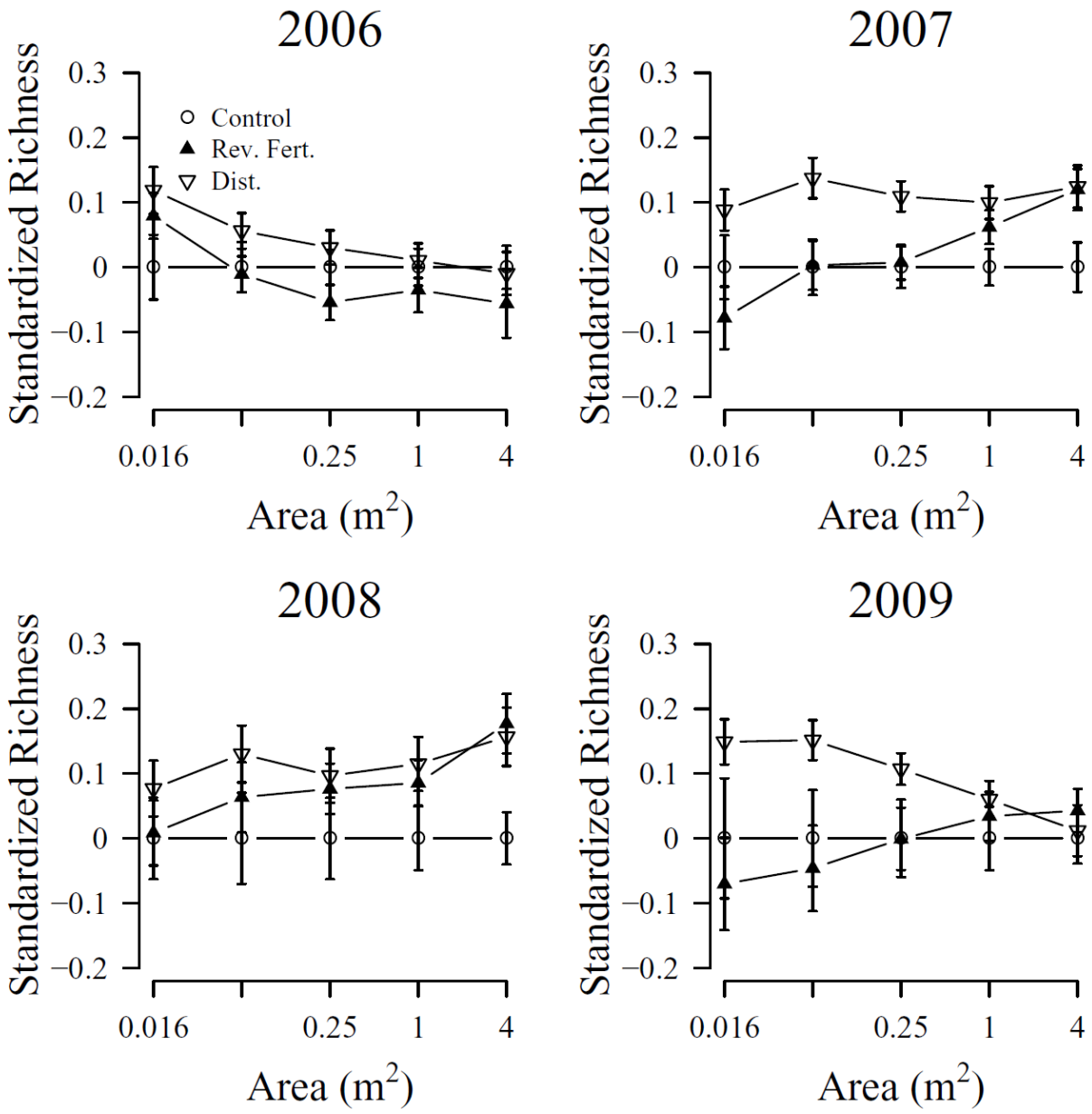


Figure 5

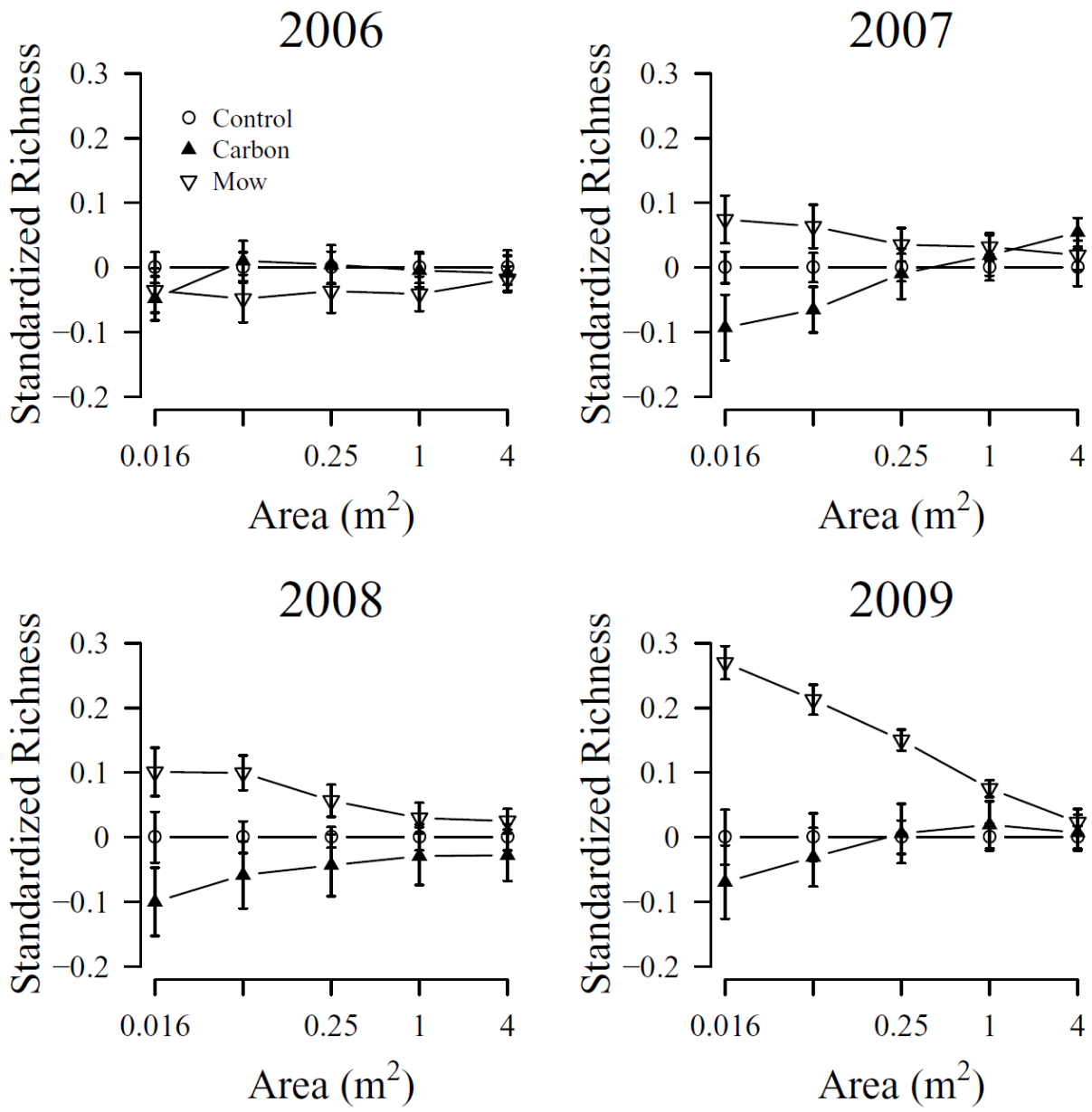


Figure 6

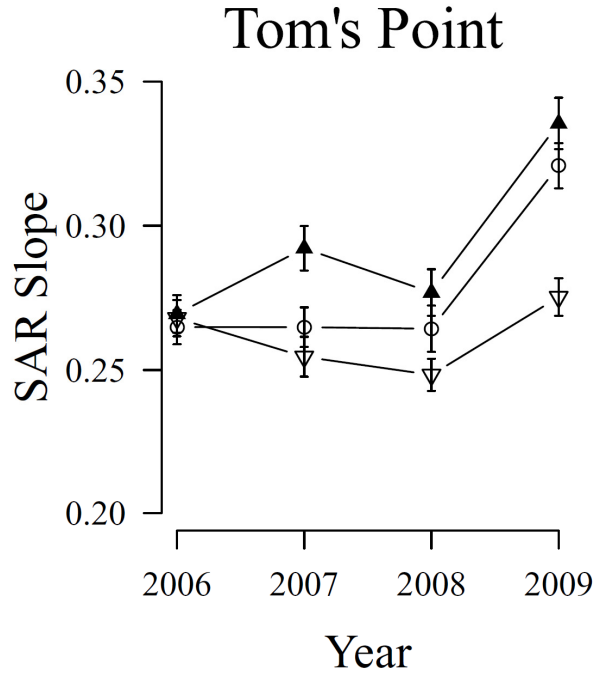
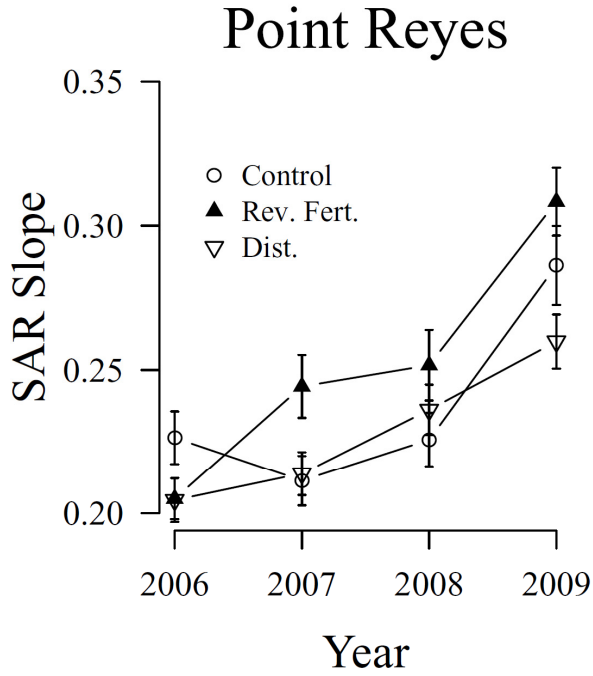


Figure 7

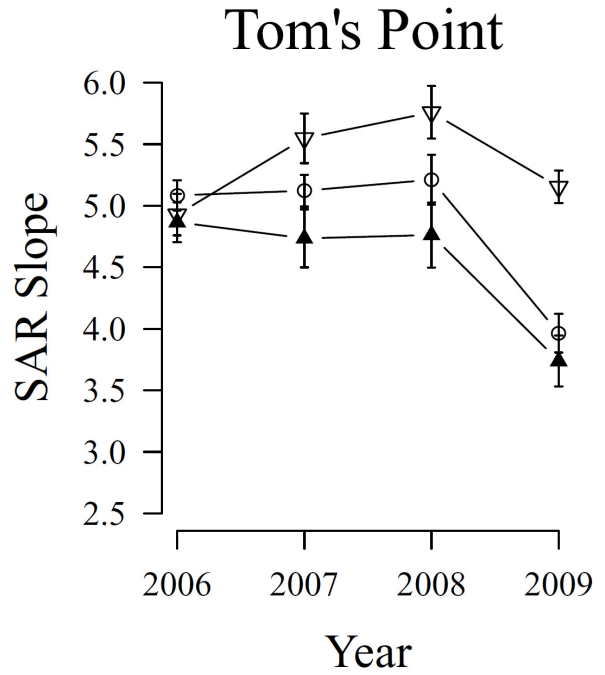
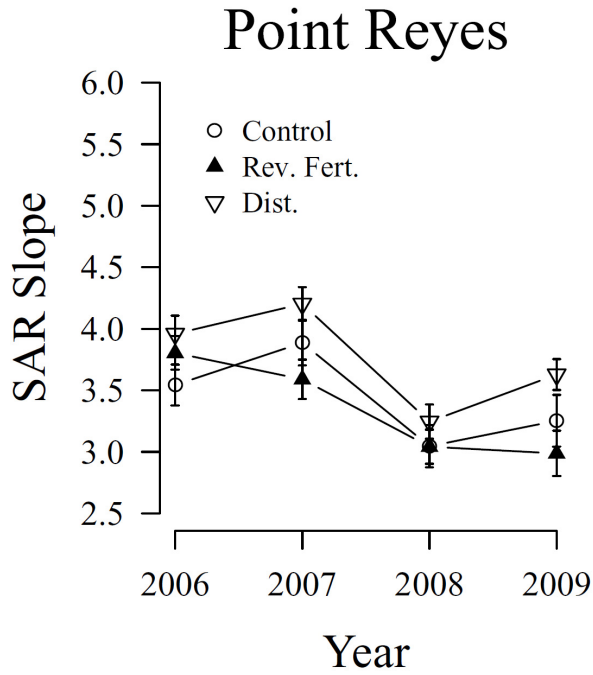


Figure 8

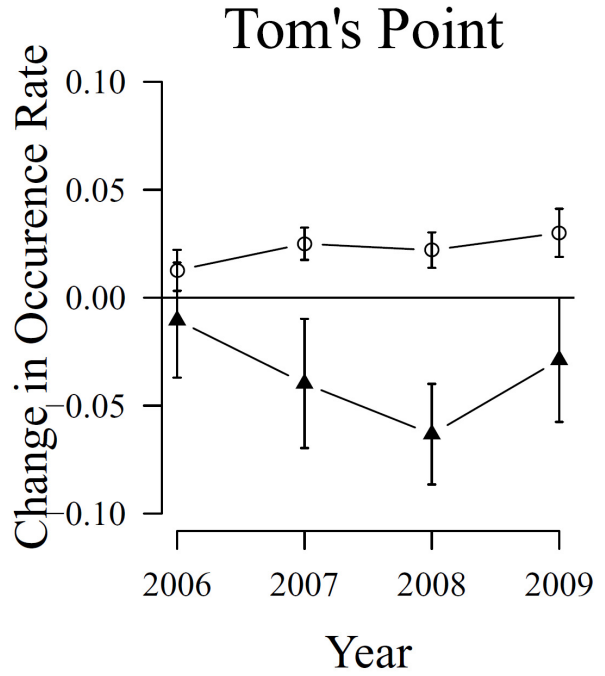
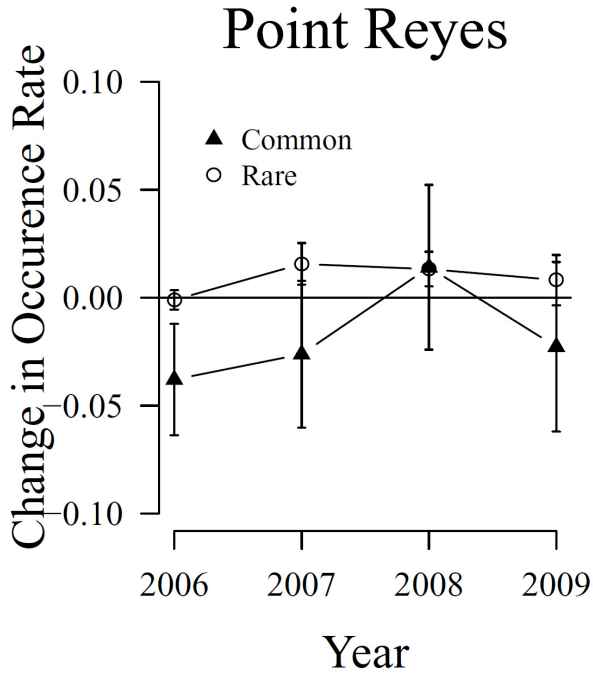


Figure 9

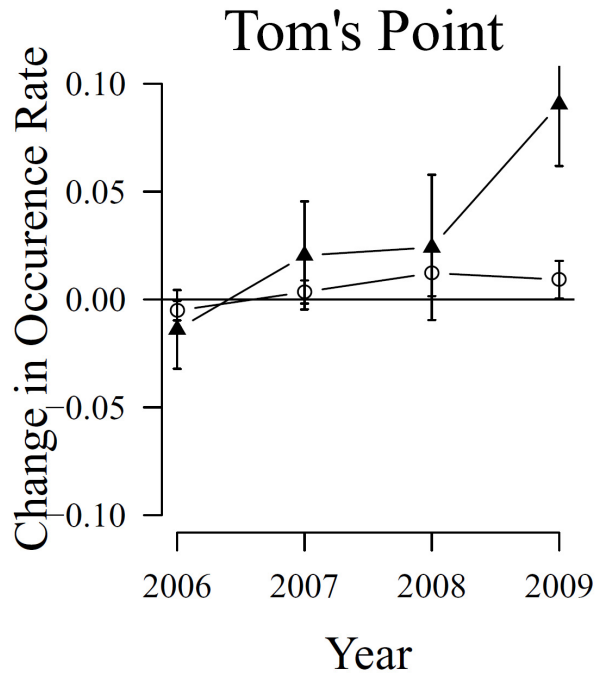
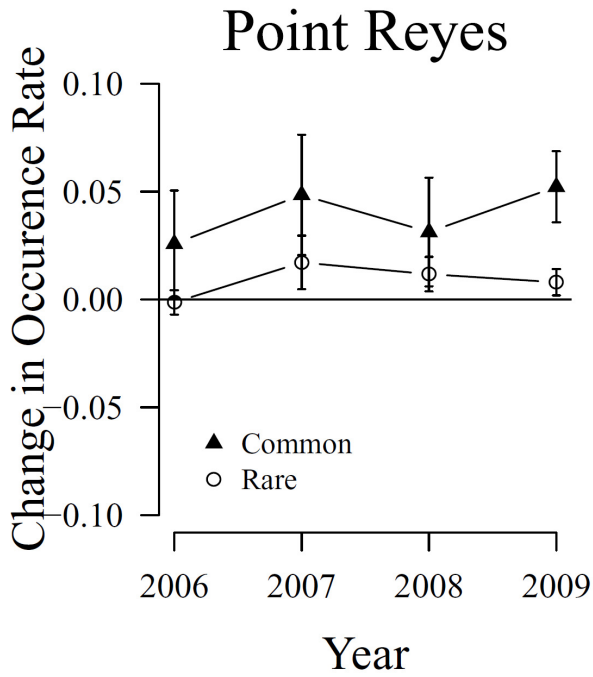


Figure 10

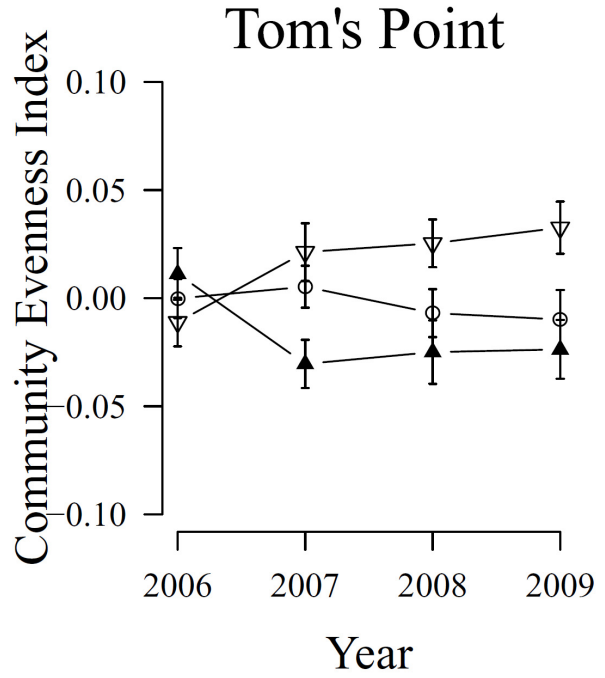
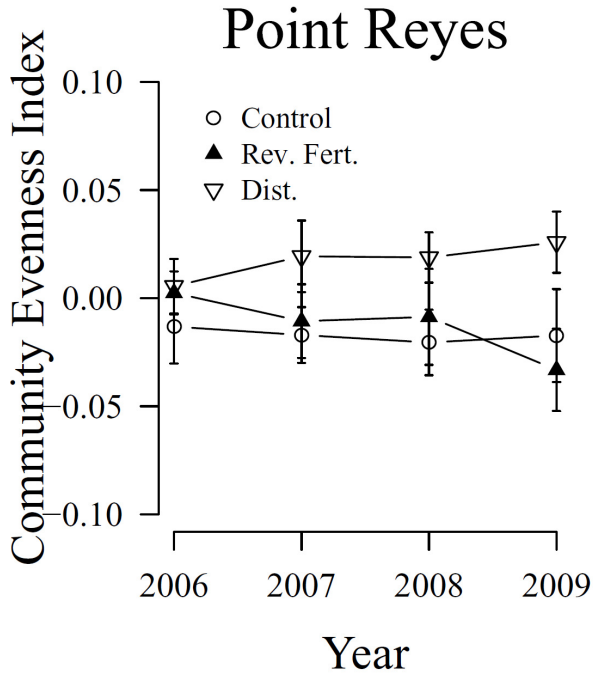


Figure 11

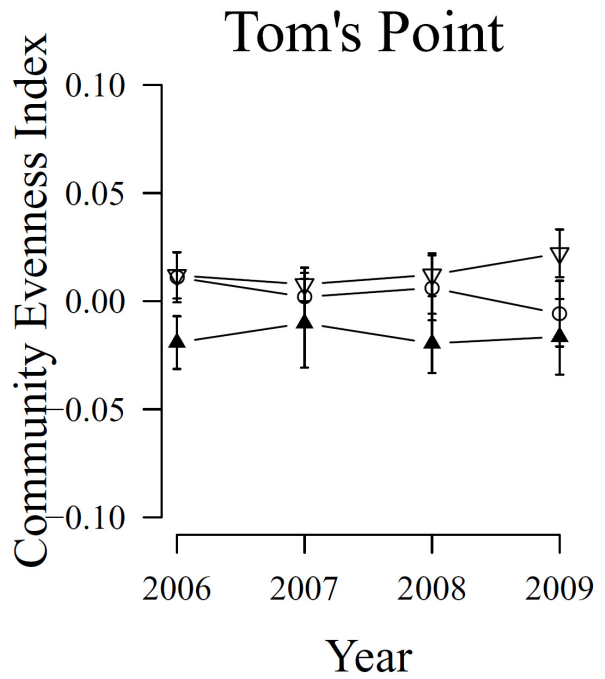
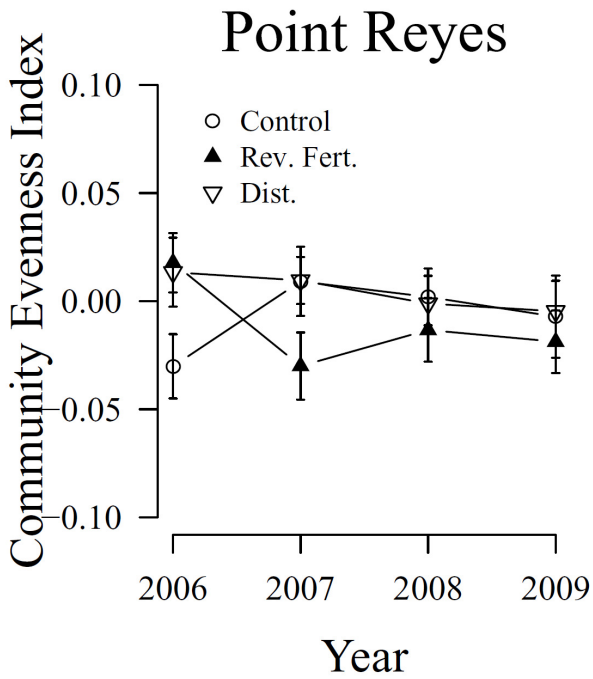


Figure 12

Chapter 4
Sweetening the plot:
Can carbon addition restore
native plant diversity?

Abstract

Many terrestrial plant communities are experiencing exceptionally high nitrogen supply rates due to human activities. This can cause a wide array of changes, including increased abundance of exotic weeds and decreased abundance of native species. Accordingly, efforts to restore native plant communities could be more successful if they included a mechanism to reduce nitrogen availability. One method to accomplish this is carbon addition, which can increase soil microbial biomass and immobilize nitrogen in microbial cells. As a result, less nitrogen is available to plants, which can reduce growth and change interactions among species, possibly favoring native species.

We examined carbon addition as a restoration tool in two heavily invaded, nitrogen-enriched coastal Californian grasslands. The treatment reduced nitrogen mineralization rates and plant productivity, but did not lead to increased abundance of native species. We examined a suite of functional traits in order to improve predictions for how species will respond to C addition. Species with small leaf areas or large seeds tended to benefit from C addition. Carbon addition was not found to be an effective means to restore native species to these grasslands, but the trait-based approach used here could prove to be a useful screening tool to assess the suitability of the treatment at other sites.

Introduction

Anthropogenic fertilization of soils is widespread and, in many cases, quite extreme. Through the application of artificial fertilizers, cultivation of nitrogen-fixing plants and combustion of fossil fuels, humans now add more fixed nitrogen to terrestrial systems than all natural sources of nitrogen fixation combined (Vitousek et al. 1997a, Schlesinger 1997). Because nitrogen is an important limiting resource for plant growth, increases in its availability often have major impacts on ecosystems (Tilman 1984, Vitousek et al. 1997b, Fenn et al. 2003, Crawley 2005). A common result of N fertilization is increased abundance of weedy exotic species (Hobbs et al. 1988, Burke and Grime 1996, Wedin and Tilman 1996, Weiss 1999, Brooks 2003, Tyler et al. 2007, Bobbink et al. 2010), perhaps because many species that are successful invaders employ weedy strategies, and are therefore better able to take advantage of high resource availability (Chapin 1980, Chapin et al. 1986, Alpert et al. 2000).

If exotic species benefit differentially from high nitrogen availability, restoration of native communities could be more successful if nitrogen levels were reduced. This can be accomplished by adding a substance with high C:N ratio to the soil. Soil microbes benefit from the added C availability, but must take up additional N from the soil to support their population growth. As long as this nitrogen remains in soil microbes, it is immobilized and unavailable to plants. Carbon addition can successfully counteract the effect of increased anthropogenic nitrogen input, reducing soil fertility and consequently plant growth (Baer et al. 2003, Averett et al. 2004, Corbin and D'Antonio 2004).

Carbon addition has been tested as a restoration tool in a number of systems including grasslands, shrublands and woodland understories (e.g. Corbin and D'Antonio 2004, Eschen et al. 2007, Zink and Allen 1998, Prober et al. 2005). Such studies have consistently found decreases in various measures of nitrogen availability and reductions in plant growth following C addition. Microbial biomass has also shown the expected increase in some studies (Baer et al. 2003, Corbin and D'Antonio 2004), but not in all (Zink and Allen 1998). However, predicting the

response of native and exotic plant species has proven more difficult (Blumenthal 2009). A number of studies have found increases in the relative abundance of native species (McLendon and Redente 1992, Maron and Connors 1996, Zink and Allen 1998, Alpert and Maron 2000, Blumenthal et al. 2003, Averett et al. 2004, Prober et al. 2005, Blumenthal 2009), while others have not (Reever Morghan and Seastedt 1999, Cione et al. 2002, Corbin and D'Antonio 2004).

This difficulty may be because, in certain systems, native and exotic species do not differ substantially from one another along plant strategy or tradeoff axes (Levine and D'Antonio 1999, Corbin and D'Antonio 2010). A species' response to C addition is likely to depend on its life history, resource allocation, and reproductive strategies (Eschen et al. 2006). So, measurements of these characteristics may improve understanding and prediction of species responses (Diaz et al. 2001, Pywell et al. 2003, Suding et al. 2005). Using easily measurable traits to predict species responses to C addition has several advantages. First, it enables a mechanistic interpretation of species responses because those responses can be linked directly to plant strategies and tradeoff axes. From a management perspective, trait data can be relatively straightforward to collect. Thus, sites could be screened fairly rapidly to determine whether the desired species have the trait states promoted by C addition.

Based on a considerable existing literature addressing the relationships of plant strategies to environmental conditions, it is possible to predict which plant traits should be associated with responses to C addition. A primary axis of differentiation among plant species runs between those with a short versus long return on investments (Chapin 1980, Reich et al. 1997, Wilson et al. 1999, Wright et al. 2004). Species with short returns exhibit rapid turnover of leaf biomass, and tend to produce thin, low density leaves with high specific leaf area (SLA, Wright and Westoby 2000, Wright et al. 2004). Because leaf construction becomes more costly when nutrients are scarce, these traits may become disadvantageous with C addition. In addition, as soil resources become more limiting, competition for light should become less important (Tilman 1988). Carbon addition has been shown to lead to increased light penetration (Baer et al. 2003), so large height and high leaf area, both traits related to light capture ability, should be less advantageous following C addition. Finally, seed mass is an important determinant of seedling success, particularly in nutrient-poor environments (Milberg et al. 1998). With reduced N availability, the additional resources provided by a large seed should become more useful (Lee and Fenner 1989).

The coastal grasslands of California provide an ideal testing ground for C addition as a restoration method. Californian grasslands are heavily invaded and enriched by anthropogenic nitrogen (Weiss 1999). While Californian grasslands were historically dominated by perennial bunchgrasses (Clements 1932, Burcham 1956), the vegetation today consists primarily of exotic annual species, mostly from the Mediterranean (Heady 1988). In addition, approximately 90% of California's perennial grasslands receive more than 5 kg N/ha/year in atmospheric nitrogen deposition, an amount sufficient to have significant ecosystem impacts (Weiss 2006). Coastal grasslands are also enriched by the native N-fixing shrub *Lupinus arboreus* (Maron and Connors 1996).

In this study, we used greenhouse and field experiments to elucidate the effects of C addition at multiple organizational scales, ranging from soil nutrient responses to individual plant growth responses, to changes in community assembly. We ask three questions: 1) does C addition have the expected effect on bacterial populations, soil nitrogen availability and plant growth, 2) do native species, as a group, benefit from C addition, and 3) can information on plant functional traits be used to help predict how species will respond to C addition? Answering

these questions will give land managers the tools to determine the suitability of C addition to accomplish management goals for particular sites.

Methods

We used two approaches to assessing the effects of C addition. These were a short-term, controlled greenhouse experiment, and a long-term field experiment. In the first, we ask how soil bacterial abundance, N availability, plant growth and plant allocation respond to C addition. In the field, we asked how these effects translate into changes in plant abundance and community composition.

Greenhouse

We used field-collected soil in the experiment to ensure that the carbon addition would act on a realistic bacterial and fungal community. Soil cores were collected near the treatment plots at Tom's Point (see *Field*, below) on April 4, 2008. Cores were approximately 25 cm deep. Upon collection, cores were immediately transferred to large cone-tainers (6.2 cm diameter, 650 ml volume, Stuewe and Sons, Inc. Tangent, Oregon), maintaining the structure of the soil, and any plants were removed. In the greenhouse, we germinated hundreds of seeds of the exotic annual grasses *Bromus diandrus* and *Bromus hordeaceus* in trays with a thin layer of potting soil. These species were selected because they are abundant at both field sites, are easily germinated in the greenhouse, and showed differing responses to the field C addition (see below). On April 28, we transplanted the seedlings to the pots and applied the sugar treatment. Seedlings were transplanted four to a pot, with either four of one species or two of each. Sugar was added to the soil surface in each pot at three levels – no sugar, 1.37 g and 2.74 g. The 1.37 g/pot treatment is equivalent to the density of sugar added to field plots (henceforth Carbon 1x), while the 2.74 g/pot treatment is twice that rate (henceforth Carbon 2x, see *Field* below).

In total, there were three levels of sugar addition, and four levels of species: no plants, four *B. diandrus*, four *B. hordeaceus*, or two *B. diandrus* and two *B. hordeaceus*. Each combination was replicated ten times, for a total of 120 experimental pots.

In order to measure bacterial and soil N responses to C addition, we collected soil samples from each soil-only pot periodically. Immediately before the sugar treatment, and each week for the following six weeks, we collected approximately 5 g of soil to a depth of 5 cm from each soil-only pot. Three grams of this sample were extracted immediately with 15 ml 2 M KCl for one hour. We filtered the extract to remove soil particles, and sent the solution to the UC Davis Agriculture and Natural Resources Analytical Lab to obtain NO₃ and NH₄ concentrations using flow injection analysis.

In addition, we preserved 0.1 g of soil in 1 ml formalin, to kill and preserve any bacteria and fungus in the soil, and prepare them for direct counting using DAPI staining (Yu et al. 1995). We sonicated the samples to detach bacteria from the soil particles and stained each sample with 3 drops of 100µg/mg DAPI solution in the dark. Following the stain, a vacuum was applied to pull the stained solution through a black GTBP filter, and the slides were wrapped in aluminum foil and stored in a dark box in a refrigerator. This method was chosen because it can identify both fungus and bacteria. However, fungal abundances proved too low to provide accurate estimates. To count the bacteria, we removed the slide from its aluminum foil wrapping in a dark room and examined it under 1000x magnification with oil immersion. We used an epifluorescent microscope with a mercury bulb to fluoresce the stained bacteria. We used an

optical grid to define “plots” on the slide surface, and counted the number of cells in 20 blindly selected grids per slide.

On May 12 and May 23, we measured every plant in the greenhouse experiment. For each plant, measurements included the maximum height of the plant, the width of the widest leaf, and the number of leaves. On June 11, we repeated all of these measurements and harvested all of the experimental plants. In addition, we separated the above-ground component of each plant from its roots. Individual above-ground components were stored and dried separately, but the roots of the individuals within a pot were inseparable, so we washed and dried the entire root mass from each pot together. After at least 48 hours of drying at 50 C, we weighed each biomass component.

The competitive interactions between the two grass species were estimated using relative competitive intensities (RCI) of each species on the other. This index describes the magnitude of interspecific competition relative to intraspecific competition, and is calculated as follows: $RCI = (M_A - M_M)/M_A$, where M_A is the average aboveground biomass of a plant of the target species grown in monoculture and M_M is the aboveground biomass of a plant when grown in competition with the other species (Keddy et al. 2002).

Field

The field study was located at two coastal California grassland sites. These were the Pierce Point Ranch at Point Reyes National Seashore and Tom’s Point, a private nature reserve owned by Audubon Canyon Ranch. Both sites were dominated by exotic species, most notably the grasses *Holcus lanatus*, *Lolium perenne* and *Bromus diandrus*, but Tom’s Point retains a greater native component (taxonomy follows Hickman 1993). Each site had scattered *Lupinus arboreus* shrubs, which have been shown to increase soil N in coastal California grasslands (Maron and Connors 1996). The two sites have been free from livestock grazing for at least 35 years, though the Point Reyes site is visited frequently by native Tule Elk (*Cervus elaphus nannodes*). The plots at Point Reyes were located at 38° 11’ 24” N, 122° 57’ 21” W, 100 m ASL, while the Tom’s Point site was at 38° 13’ 7” N, 122° 57’ 4” W, 20 m ASL. Weiss (2006) estimated that these sites receive between 6 and 8 kg/ha/year total N deposition.

In 2005, we established 16 replicate treatment plots and 16 control plots at each site. Plots were 5 x 5 m at Point Reyes, and 4 x 4 m at Tom’s Point, because of space limitations. Beginning in October 2005 and every six months thereafter, we applied the carbon addition treatment to the appropriate plots. Carbon was added as sucrose at 450 g/m² (189.5 g C/m²), except the original application, which was 170 g sucrose/m² and 360 g sawdust/m² (approximately 240 g total C/m²). Half of the plots of each treatment type also received a mix of native grass seed each fall. However, the seed addition treatment had a negligible effect on the abundance of seeded species, so that treatment is ignored here.

We sampled the plant community in the summers of 2006, 2007, 2008 and 2009. In the center of each treatment plot, we established a 2 x 2 m sampling plot. This plot was gridded into 16 50 x 50 cm subplots. We then assessed the presence or absence of all plant species within each of these subplots. In addition, in the summers of 2008 and 2009, we estimated the percent cover of each plant species occurring in the middle four subplots. This allows two measures of a species’ abundance within a plot: 1) a spatial abundance measure, the occurrence rate of the species in the 16 subplots, and 2) the relative abundance of the species, based on percent cover estimates. In 2009, cover estimates also included estimates of bare ground.

On March 31, 2006, shortly after the spring C addition, we collected three 15 cm deep, 2 cm diameter soil cores from carbon-treated and control plots, in order to measure net N mineralization rates. We bulked the samples, extracted half of each soil sample immediately with 2 M KCl, and incubated the other half in the lab for two weeks. Then, we extracted the remaining soil samples with 2M KCl. These extracts were analyzed for NO₃ and NH₄ concentrations by the UC Davis Agriculture and Natural Resources Analytical Lab using the flow injection analyzer method. Net N mineralization was calculated as the amount of NH₄ + NO₃ in incubated soils minus the amount in soils extracted immediately. At the end of the summers of 2006, 2008 and 2009, we clipped all standing plant biomass from two 25 x 25 cm squares (or 50 x 50 cm squares, in 2006) within each treatment plot. We then dried and weighed these samples.

Traits

Between April and June, 2009, we collected data on functional traits of plant species occurring in experimental plots. For species that were sufficiently abundant, we sampled one individual from each treatment and control plot at each site. We sampled the first mature individual of each species encountered in a search beginning from a random corner of each treatment plot. In this ideal case, we obtained 16 representatives of a species from each site and treatment, for a total of 64 samples. However, many species were not present in all plots. In such cases, we took samples from up to two individuals from each plot where the species could be found, in order to come as close as possible to the goal of obtaining 64 samples per species.

We measured the height of the highest photosynthetic surface from each individual, and then collected one fully expanded, green leaf. We immediately measured the thickness of the leaf lamina using a high-precision caliper, avoiding any major leaf veins. Each leaf was stored in an individually labeled coin envelope and refrigerated. Within 24 hours of collection, we took a photograph of each leaf against a white background. We then determined the surface area of each leaf using the ImageJ (Rasband 2009) image analysis software. Finally, leaves were oven-dried at 50 C for at least 48 hours, then weighed individually on a high-precision balance. Thus, the traits collected from each individual were the height, leaf thickness, leaf area and leaf mass. In addition to these raw values, we calculated specific leaf area (leaf area per unit mass) and leaf density (leaf mass per unit area, divided by leaf thickness). For each species and each trait, we then calculated a species mean trait value from all control plot samples, all C addition plot samples, and all samples combined.

Species were also classified according to several categorical traits, including growth form (graminoid or not), lifespan (annual or not), nitrogen fixing ability and origin (native or exotic). Finally, we supplemented these data with data on species' mean seed sizes, from the Kew Gardens Seed Information Database (Liu et al. 2008); most seed size data for the California species in this database are originally from Baker (1972).

Analysis

We first examined how species' traits differed between control and C addition plots. For each species and trait, we calculated a treatment effect size by taking the difference between that species' mean trait value in carbon plots and the mean value in control plots. We used only species with measurements from at least two individuals in each plot type. For each trait, we then performed a one-sample t-test to determine whether these treatment effect sizes differed

collectively from zero. All quantitative trait values were log-transformed prior to analysis to improve normality.

We tested for overall differences between species mean trait values of native and exotic species. Considering one trait at a time, we performed t-tests comparing the trait means of native species to exotic species. For categorical traits, we instead performed a chi-squared test. In addition, we tested for multivariate differences between native and exotic trait means using the multi-response permutation procedure (MRPP, Mielke and Berry 2001, Cai 2006).

We took two approaches to examining the ability of functional traits to explain changes in the plant community following carbon addition. In the first, species are the unit of replication (species-based), while in the second, plots are the unit of replication (plot-based).

Species-based

For the species-based method, we calculated a treatment effect size for each species, then examined the relationship between these effect sizes and the species' traits. Effect sizes were calculated for each year of the experiment as the log of the ratio of the species' occurrence rate in carbon plots to the species' occurrence rate in control plots. Occurrence rate was defined as the proportion of 50 x 50 cm sampling cells occupied by the species. As there are 16 sampling cells in each treatment plot, and 16 plots of each treatment and site combination, these occurrence rates took the values of the integers between 0 and 256 divided by 256.

We then performed repeated-measures ANCOVAs for each continuous trait and repeated-measures ANOVAs for each categorical trait, examining that trait's ability to predict these effect sizes across all years of the experiment. In these analyses, site was treated as a fixed factor, trait value as a covariate (or factor, in the case of categorical traits) and treatment effect size as the response variable, with repeated measures of species through years. We also performed a multivariate analysis, to test the ability of multiple traits considered together to predict species' responses. In this analysis, we first used a PCA to reduce the dimensionality of species traits, then used backwards and forwards model selection procedures (using the R function *step*) to select only those variables and interaction terms that substantially improved model fit. The best model was selected using AIC values (Akaike 1974).

Plot-based

We also conducted an analysis at the plot level. In this approach, we calculated the mean value of each trait within a plot, weighted by the abundance of each species. Two kinds of abundances were used. The first was a spatial abundance measure, the occupancy rate of a species within 0.25 m² subplots within the sampling plot. The second was based on visual estimates of percent cover for all species, taken in 2008 and 2009.

We then tested for treatment effects on plot mean values for each trait using repeated-measures ANOVA. Site and treatment were treated as fixed factors and community mean trait values were measured from plots repeatedly through years. These tests were performed separately for each trait, and separately for occurrence-based and abundance-based means.

Finally, because treatment and control plots might differ little with respect to any single trait, but greatly in multivariate trait space, we performed a comparable multivariate analysis, addressing all traits simultaneously. To examine the differences between control and treatment plots in multivariate trait space, we used the MRPP (Mielke and Berry 2001, Cai 2006). We then used non-metric multidimensional scaling to visualize multivariate differences among plots in a two-dimensional space.

Results

Greenhouse

Sugar addition significantly reduced extractable NH_4 and NO_3 concentrations relative to control pots (RM ANOVA, $F_{2,26} = 14.667$ and 58.665 , $P < 0.00001$, fig. 1). Microbial abundance increased dramatically with C addition (ANOVA on last time point, $F_{2,25} = 4.026$, $P = 0.0305$, fig. 2). The decrease in extractable soil N was accompanied by a decrease in plant growth, including reduced height, leaf width, leaf number, aboveground biomass and belowground biomass (fig. 3A,B; Table 1). In addition, *B. hordeaceus*, but not *B. diandrus*, showed greater relative allocation to root growth with sugar addition (fig. 3C). For most growth metrics, the Carbon 2x treatment produced greater growth reduction than Carbon 1x, though the relationship was generally non-linear.

The competitive interaction between the two *Bromus* species was very sensitive to changes in soil fertility. Under ambient conditions, individuals of both *B. hordeaceus* and *B. diandrus* grew better in competition with *B. hordeaceus* than they did with *B. diandrus*, suggesting that *B. diandrus* is the stronger competitor. However, with increasing degrees of carbon addition, the interaction between the two species became increasingly positive (fig. 3D), with the result that the mixed species treatment exhibited significant overyielding relative to either monoculture in the Carbon 2x treatment (fig. 3A,B). At this point, we do not understand the mechanism of this overyielding.

Field

Carbon addition reduced N mineralization rates in soils at both sites by approximately 90% (ANOVA $F_{1,28} = 162.4$, $P < 0.00001$, fig. 4A). This reduction led to a decrease in productivity in these plots, with C addition plots typically showing 20-30% reductions in standing crop (RM ANOVA, $F_{1,28} = 13.00$, $P = 0.0012$, fig. 4B). In 2009, there was 2.5 times more bare ground in C addition plots relative to the controls (control mean 5.9%, carbon mean 14.9%, ANOVA $F = 21.28$, $P = 0.00002$).

Species responses to the treatment ranged from strongly positive to strongly negative. At Point Reyes, species that increased include the native N-fixer *Lupinus bicolor*, exotic N-fixer *Trifolium subterraneum* and exotic annual grass *Briza maxima*. Species that strongly decreased in abundance included *Bromus hordeaceus* and *Geranium dissecta*, an exotic annual grass and forb, respectively. At Tom's Point, increasing species included the native forb *Eschscholzia californica* and native N-fixer *Trifolium bifidum*, as well as the exotic forb *Linum bienne*. Several other native species did respond positively to C addition at Tom's Point, including *Lupinus bicolor*, *Bromus carinatus* and *Danthonia californica*. *Pteridium aquilinum*, a native fern, and *Rubus ursinus*, a native forb, decreased notably with C addition at Tom's Point (Appendix 1).

Carbon addition had no effect on the relative abundance of native species as a group, calculated from occurrence rates (RM ANOVA $F_{1,59} = 0.0105$, $P = 0.9186$) or percent cover ($F_{1,59} = 0.0053$, $P = 0.9420$). Similarly, neither the summed occurrence rates of annual species nor grasses changed with C addition for either occurrence-based (RM ANOVA $F_{1,59} = 0.1298$, $P = 0.7199$ and $F_{1,59} = 0.5378$, $P = 0.4663$, respectively) or cover-based analyses ($F_{1,59} = 0.2255$, $P = 0.6367$ and $F_{1,59} = 1.084$, $P = 0.3020$). Nitrogen-fixing plants, in contrast, responded positively to C addition (RM ANOVA $F_{1,59} = 20.05$, $P < 0.0001$). This effect became increasingly apparent

through time (year-by-treatment interaction $F_{1,185} = 17.26$, $P < 0.0001$), and was particularly strong at Point Reyes (site-by-treatment interaction $F_{1,59} = 5.659$, $P = 0.0206$).

Quantitative traits

Plant traits were plastic in response to C addition. Plants growing in C addition plots tended to have smaller individual leaf area ($t_{38} = -3.550$, $P = 0.0010$), leaf mass ($t_{38} = -2.062$, $P = 0.0461$) and specific leaf area ($t_{38} = -2.189$, $P = 0.0349$), reduced height ($t_{38} = -4.836$, $P < 0.0001$), and higher leaf density ($t_{38} = 2.872$, $P = 0.0066$, fig. 5).

We asked whether mean trait values differ between native and exotic species, as groups. Native and exotic species did not differ significantly in mean values for any of the quantitative species traits (t test, $P > 0.05$), nor were they separable in multivariate space (MRPP $P = 0.499$). Native species were not more or less likely than exotic species to be grasses or N fixers (chi-squared test, $P > 0.1$), but were more likely to be perennial (chi-squared test $\chi^2 = 10.68$, $P = 0.0011$).

Species-based

The univariate analysis of trait predictors of a species' treatment response revealed two traits with predictive power. At Tom's Point, leaf area was negatively correlated with response to C addition (RM ANCOVA $F_{1,50} = 5.617$, $P = 0.0217$, fig. 6), while at Point Reyes, seed mass was a positive predictor of response (RM ANCOVA $F_{1,48} = 5.973$, $P = 0.0183$, fig. 6). To examine the predictive ability of multiple traits considered together, we first performed a principal components analysis on all seven quantitative traits. The first three PCA axes explained 86% of the variation in the trait data, and can be interpreted as a measure of leaf size (including area, thickness and mass), a combination of height and leaf density, and seed mass (Table 2). At Tom's Point in 2007 and 2008, the general measure of leaf size (PCA axis 1) was negatively correlated with treatment responses. At Point Reyes in 2008 PCA axis 3 was negatively correlated with treatment responses, indicating that larger seeded species showed a positive response.

Plot-based

The plot-level analysis revealed similar patterns. Using occurrence-based plot trait means, seed mass significantly increased in treatment plots (RM ANOVA, $F_{1,59} = 9.109$, $P = 0.0036$, fig. 7). Especially at Point Reyes, carbon addition caused a shift towards large-seeded species, with increasingly strong effects through time (treatment-by-year interaction, $F_{3,185} = 9.468$, $P < 0.0001$). Individual leaf area and thickness showed significant treatment-by-site interactions, with carbon addition tending to favor thicker- and larger-leaved species at Point Reyes and thinner- and smaller-leaved species at Tom's Point (thickness interaction term, $F_{1,59} = 4.412$, $P = 0.0400$, area interaction term, $F_{1,59} = 4.691$, $P = 0.0308$). The analysis based on visually estimated relative abundance revealed several additional significant treatment by year interactions, including leaf area ($F_{1,59} = 5.650$, $P = 0.0207$, fig. 8), leaf mass ($F_{1,59} = 6.138$, $P = 0.0161$, fig. 9) and height ($F_{1,59} = 8.092$, $P = 0.0061$, fig. 10).

Control and treatment plots at Point Reyes in 2007 and 2009 occupied distinct locations in trait space (MRPP $P = 0.042$ and $P = 0.001$, respectively, fig. 11). At Tom's Point, control and treatment plots were separable only in 2009 (MRPP $P = 0.033$, fig. 12).

Discussion

We asked three questions in this study: 1) does C addition affect N availability, microbial population and plant growth, 2) do native species benefit from C addition, and 3) can species functional traits predict their responses to C addition?

Carbon addition had the expected effects on soil properties and productivity, both in the greenhouse and in coastal Californian grasslands. In both systems, C addition reduced plant-available N and consequently plant growth. Hence, C addition appears to be an effective method of reversing anthropogenic nitrogen fertilization. To the extent that exotic species are more nitrophilic than native species, C addition should also be a useful tool to restore native species.

While C addition did alter competitive interactions and particular species did show very different responses to C addition, there was no evidence that native species benefited at the expense of exotic species. This contrasts with some previous results (McLendon and Redente 1992, Zink and Allen 1998, Alpert and Maron 2000, Blumenthal et al. 2003, Averett et al. 2004, Prober et al. 2005, Blumenthal 2009), but may be expected in systems like coastal Californian grassland, where functional differences between native and exotic species were not detected in this study (see also Corbin and D'Antonio 2010). Thus, the utility of carbon addition as a restoration measure may depend on the existence of substantial functional differences between native and exotic species that could drive differential responses of the two groups. For example, these conditions might be met in Midwestern prairies where the native prairie species are often slow-growing relative to exotic species (Averett et al. 2004), or when the natives and exotics represent clearly distinct functional groups, such as shrubs and grasses (Zink and Allen 1998).

However, in a nearby grassland with similar species composition, Alpert and Maron (2000) found that C addition strongly reduced exotic species biomass, particularly that of exotic grasses. Unlike Tom's Point and Point Reyes, however, the exotic grasses at that site are all annual species, whereas the native graminoids were exclusively perennials. This functional difference between native and exotic species may partially explain the differential responses of the two groups but is not a completely satisfactory explanation for the discrepancy between these studies, as whether or not a species was annual also was not predictive of its response to C addition in this study.

Traits

Plasticity

Carbon addition resulted in shorter plants, with smaller and denser leaves. The greenhouse experiment also revealed that *B. hordeaceus* can shift growth allocation to roots in response to carbon addition, while *B. diandrus* maintains relatively constant root:shoot ratios. This is consistent with previous results that suggest that many, but not all, species shift allocation away from roots with increasing soil fertility (Reynolds and D'Antonio 1996). SLA decreased with carbon addition, which was caused by an increase in leaf density, rather than a decrease in leaf thickness (Niinemets 2001).

These shifts, combined with changes in community composition, may have important consequences for ecosystem processes (Chapin 2003, Diaz et al. 2007). For example, reduced plant height may lead to greater light penetration to the soil (Baer et al. 2003), leading to warmer, drier soil. We also observed a decrease in specific leaf area and increase in leaf density, which could lead to reduced decomposition rates in C addition plots (Cornwell et al. 2008).

Predictive ability

The traits that provided the strongest predictions of treatment response, in both univariate and multivariate analyses, were seed mass and leaf area. At Point Reyes, seed mass was positively correlated with response to C addition, while at Tom's Point, leaf area was negatively associated with response to C. At the plot scale, these effects translated into significant shifts in community composition towards larger-seeded and, in the last year of the experiment, smaller-leaved and taller species in the treatment plots. Interestingly, this shift of community composition towards species with large mean heights was counteracted with plastic responses of species towards shorter stature with C addition.

The directions of these trait shifts were partially consistent with our hypotheses. We predicted that large leaves, which are advantageous in competition for light, would be less beneficial when soil resources are scarce, and that large seeds would be more so. Both of these predictions proved correct, though only at Point Reyes and Tom's Point, respectively. Nitrogen-fixing plants, whose ability to fix nitrogen becomes increasingly valuable as soil resources are reduced, also showed the expected increase following C addition.

More surprising were several traits that did not predict species responses. SLA, which is an important trait with respect to both plant investment strategy and light capture, was not a good predictor of species responses. Neither were the related traits leaf thickness and density. Plant height, growth form and lifespan were similarly weak predictors. These negative results could be due to limited numbers of species at the sites, which yielded limited statistical power. It is also possible that the most important response traits were not measured in this study (for example, leaf %N or rooting depth), leaving little explanatory power for the measured traits.

When is C addition a good management decision?

This study identified several native species that respond positively to C addition, including *Danthonia californica*, *Eschscholzia californica*, *Bromus carinatus* and *Lupinus bicolor*. If these species are the target of restoration efforts, C addition is likely to be an effective tool. On the other hand, increases in these native species are likely to be paired with decreases in other native species, such as *Elymus glaucus*, *Rubus ursinus* and *Monardella villosa*, and increases in exotic species such as *Avena barbata*, *Anagallis arvensis* and *Erodium botrys*.

A major strength of the trait-based approach here is that predictions can be more general than how particular species should respond. By using easily measurable, nearly universally applicable traits, we can generalize the results of this study easily to predict how species at other sites should respond to C addition. In particular, we can tentatively predict that nitrogen-fixers and large-seeded, small-leaved species should benefit most from C addition. If the restoration target species are, on average, larger-seeded and smaller-leaved than others, these results suggest that carbon addition may be an appropriate restoration tool. On the other hand, if the target species do not differ from non-target species in seed and leaf size, as they did not in this system, carbon addition might not differentially benefit those target species.

Conclusion

Carbon addition had effects at all organizational levels examined, from increasing bacterial abundance to reducing N availability and plant growth, to changing plant traits and competitive interactions, to shifting patterns of abundance in two grassland communities. Species' traits successfully predicted their response to C addition, and showed shifts that were generally consistent with previous theory. However, native species did not benefit from C

addition relative to exotic species, likely because functional differences between the two groups were very minor at these sites.

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Table 1: Summary of greenhouse results. For each species in the study and each treatment, the mean (and standard error) of five metrics of plant growth are shown. Across all metrics of plant size, both *Bromus diandrus* and *Bromus hordeaceus* showed reduced growth with increasing degrees of carbon addition.

Species	Treatment	Shoot mass (g)	Root mass (g)	Height (cm)	Leaf width (cm)	Number of leaves
<i>B. diandrus</i>	No Carbon	0.104 (0.04)	0.291 (0.18)	24.3 (0.02)	0.44 (0.02)	7.45 (0.65)
<i>B. diandrus</i>	Carbon 1x	0.025 (0.01)	0.079 (0.28)	15.6 (0.02)	0.27 (0.01)	4.45 (0.17)
<i>B. diandrus</i>	Carbon 2x	0.02 (0.01)	0.046 (0.21)	14 (0.02)	0.25 (0.01)	4.1 (0.27)
<i>B. hordeaceus</i>	No Carbon	0.088 (0.02)	0.168 (0.21)	24.6 (0.01)	0.35 (0.04)	7.18 (0.46)
<i>B. hordeaceus</i>	Carbon 1x	0.02 (0.01)	0.051 (0.26)	16.9 (0.01)	0.21 (0.01)	4.9 (0.16)
<i>B. hordeaceus</i>	Carbon 2x	0.011 (0.01)	0.038 (0.19)	10.8 (0.02)	0.19 (0.01)	4.89 (0.18)

Table 2: Principal components analysis of species traits. The first axis, explaining 44% of the variation among the seven traits, describes a species' leaf size, including area, mass and thickness. The second axis, explaining 28% of the variation, is correlated with short stature and thin leaves. The third axis primarily describes seed mass, and explains 14% of the variation. Together, these three axes explain nearly 86% of the variation among species in these seven traits.

Trait	PC1	PC2	PC3
Leaf Area	0.539	0.013	-0.004
Height	0.119	-0.520	-0.193
Leaf Thickness	0.493	0.142	0.256
Leaf Mass	0.537	-0.137	0.068
Specific Leaf Area	-0.174	0.600	-0.284
Leaf Density	-0.304	-0.572	0.014
Seed Mass	0.203	-0.057	-0.901
Prop. of Var. Explained	0.438	0.279	0.14

Figure 1 Responses of soil NH₄ and NO₃ through time to carbon addition in the greenhouse experiment. The carbon addition treatment was applied immediately after the week 0 sample was taken. Both carbon addition treatments (Carbon 1x = 1.37 g/pot, Carbon 2x = 2.74 g/pot) reduced extractable soil NH₄, NO₃ significantly relative to control levels. The reduction in NH₄ was less drastic and shortest-lived, but the NO₃ reduction persisted throughout the experiment.

Figure 2 Response of soil microbial abundance to carbon addition, through time. The carbon addition treatment was applied immediately following the measurement in week 1. Bacterial abundance responded quickly and positively to C addition, with stronger abundance increases with greater carbon addition.

Figure 3 Responses of plant growth, allocation and competition in the greenhouse experiment of C addition. After 6 weeks, carbon addition reduced both aboveground and belowground biomass of monocultures of *Bromus diandrus* and *Bromus hordeaceus* and mixtures of the two. *B. hordeaceus*, but not *B. diandrus*, shifted more of its growth allocation belowground in response to C addition. *B. diandrus* was a strong competitor in the control treatment, but became strongly facilitative in the Carbon 2x treatment.

Figure 4 Responses of N mineralization and standing biomass to C addition in the field. Carbon addition reduced nitrogen mineralization rates and standing crop at both field sites.

Figure 5 Plasticity of six traits of 39 plant species in response to carbon addition. The treatment effect is the difference between the log mean trait value for a species from C addition plots, minus its log mean value from control plots. Grey bars indicate treatment effects across all 39 species that differ significantly from 0 (t test). The heavy bar represents the median treatment effect size, the box indicates the 25th and 75th quantiles, and the error bars represent the full range of treatment effect sizes.

Figure 6 Species-based analysis of the relationship between traits and carbon addition treatment effect size. At Tom's Point, species with small leaves tended to increase in response to C addition, while large-seeded species at Point Reyes tended to increase. The points represent all species treatment effect sizes across all four years of the study at each site. The four regression lines on each plot are based on the data from each of the four years – increasingly dark lines are from later years (2006 = lightest line, 2009 = darkest line).

Figure 7 Changes in mean plot seed mass, weighted by occurrence frequency (A) and percent cover (B). Seed masses were significantly larger at Point Reyes, but both sites showed an increase in plot mean seed mass with C addition, particularly in 2009.

Figure 8 Changes in mean plot individual leaf area, weighted by occurrence frequency (A) and percent cover (B). The analysis based on occurrence frequencies revealed no treatment effects or interactions involving treatments, but the cover-based analysis showed a significant year-by-treatment interaction, with a shift towards larger-leaved species in 2009, particularly at Point Reyes.

Figure 9 Changes in mean plot individual leaf mass, weighted by occurrence frequency (A) and percent cover (B). The analysis based on occurrence frequencies revealed no treatment effects or interactions involving treatments, but the cover-based analysis showed a significant year-by-treatment interaction, with a shift towards larger-leaved species in 2009, particularly at Point Reyes.

Figure 10 Changes in mean plant height, weighted by occurrence frequency (A) and percent cover (B). The analysis based on occurrence frequencies revealed no treatment effects or interactions involving treatments, but the cover-based analysis showed a significant year-by-treatment interaction, with a shift towards taller species in 2009.

Figure 11 Non-metric multidimensional scaling plots comparing control (open circle) and carbon addition (filled triangle) plots at Point Reyes, across the four years of the experiment. The mean and standard deviation relative to both NMDS axes are shown with a large symbol and error bars. The vectors correspond to leaf area (A), leaf mass (M), specific leaf area (SLA), leaf thickness (T), leaf density (D) and seed mass (Seed). The P values were obtained using a permutation test (MRPP). Control and C addition plots occupied distinct regions of trait space at Point Reyes in 2007 and 2009.

Figure 12 As figure 11, but for Tom's Point. Control and C addition plots were distinguishable in 2009, with C addition plots tending to contain larger-seeded species.

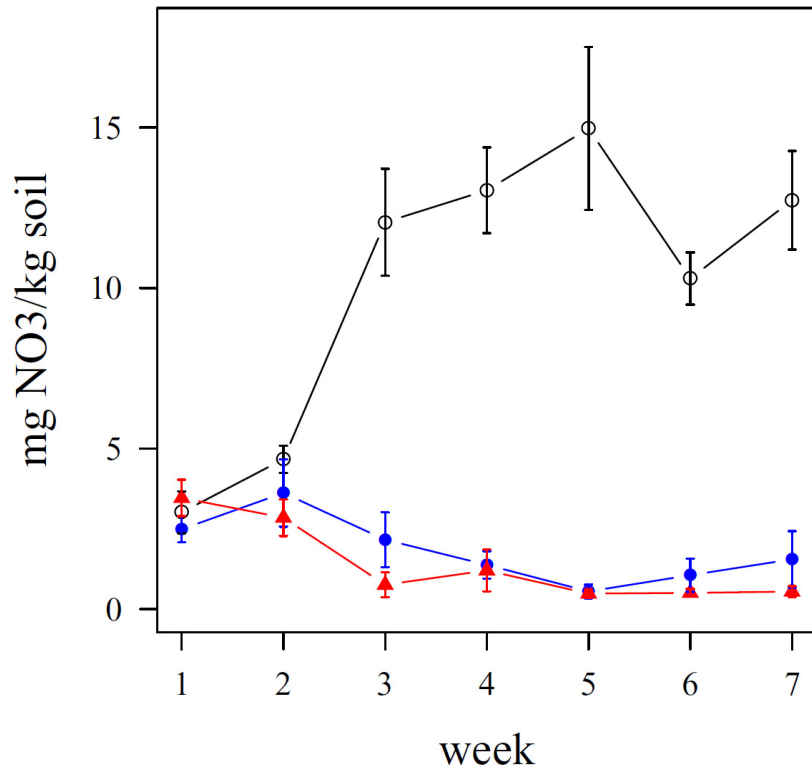
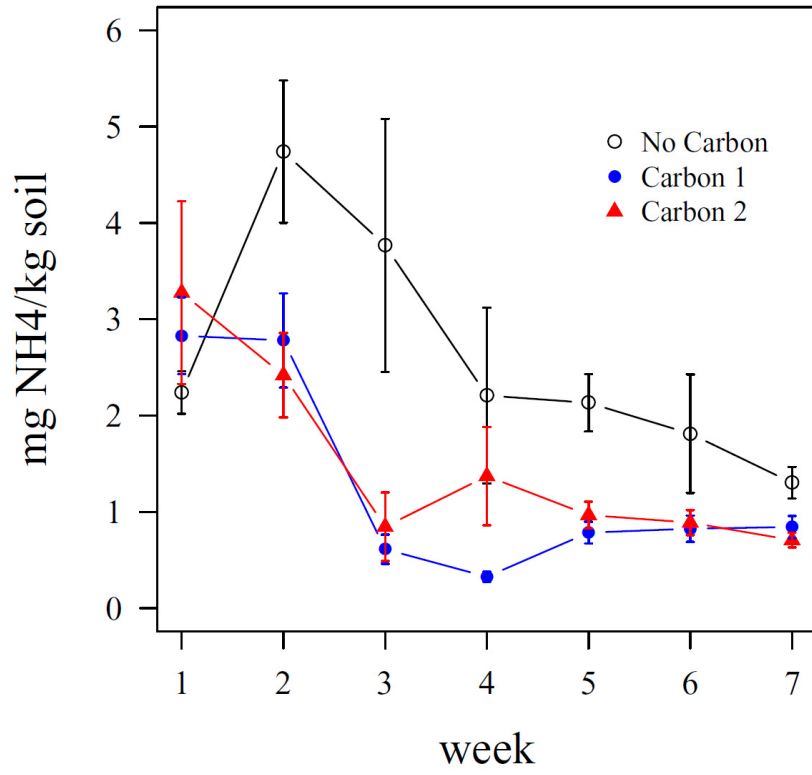


Figure 1

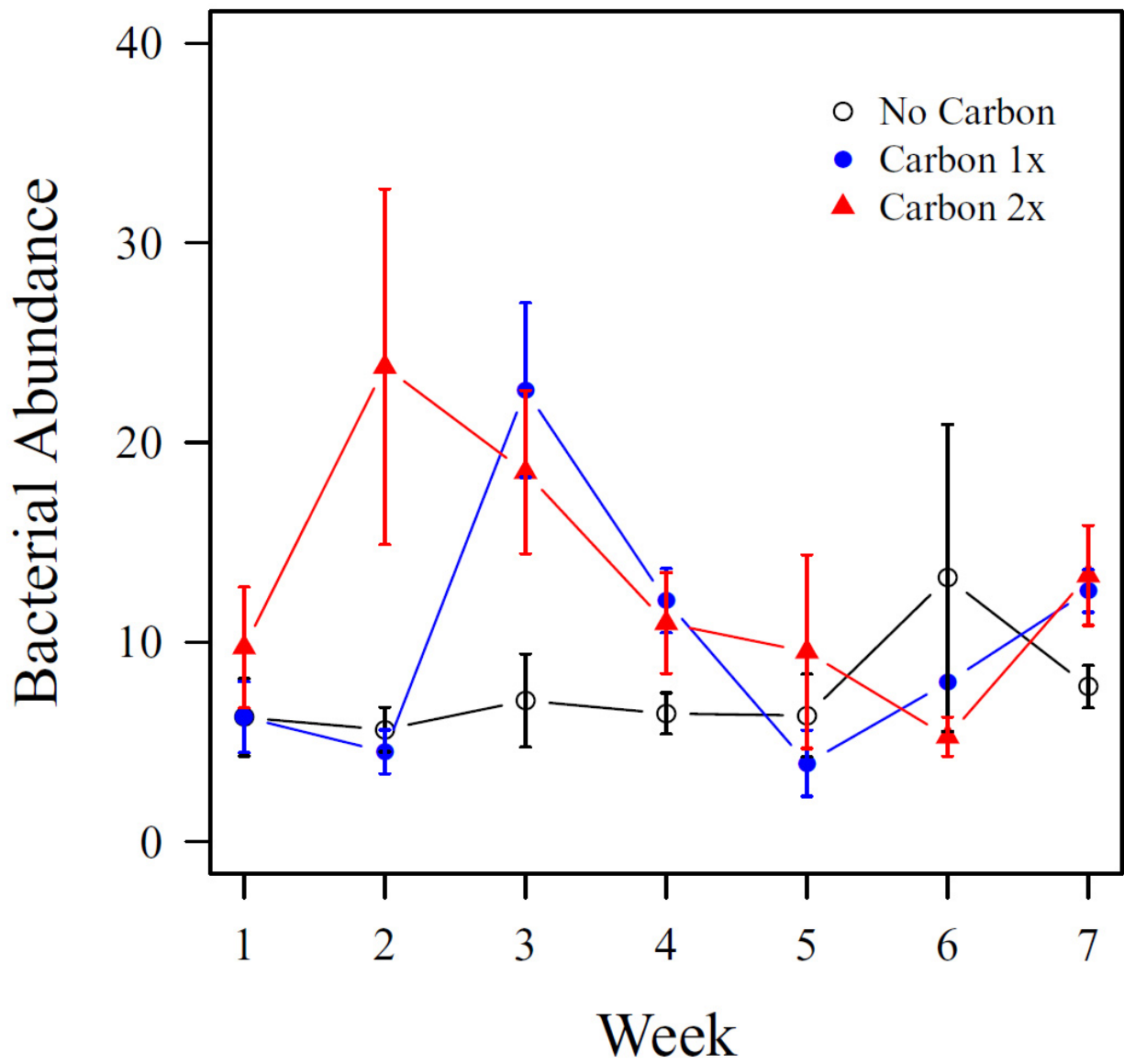


Figure 2

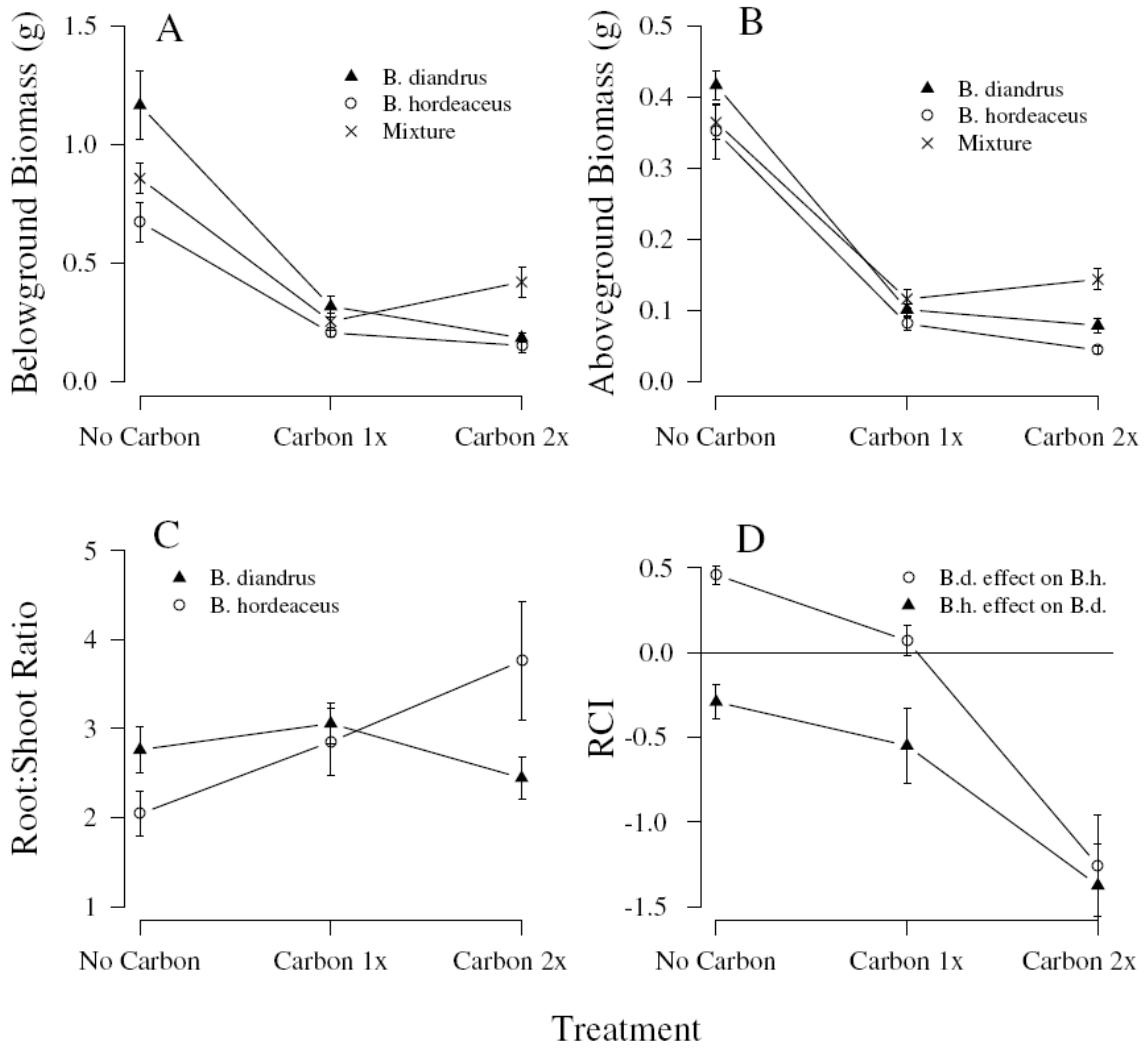


Figure 3

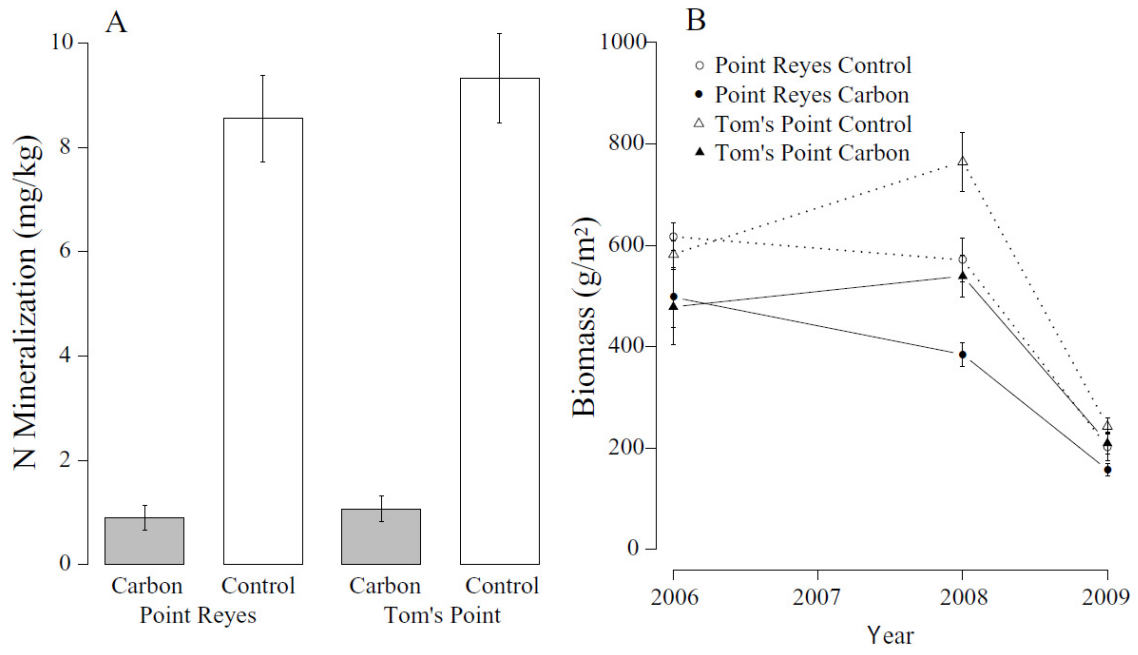


Figure 4

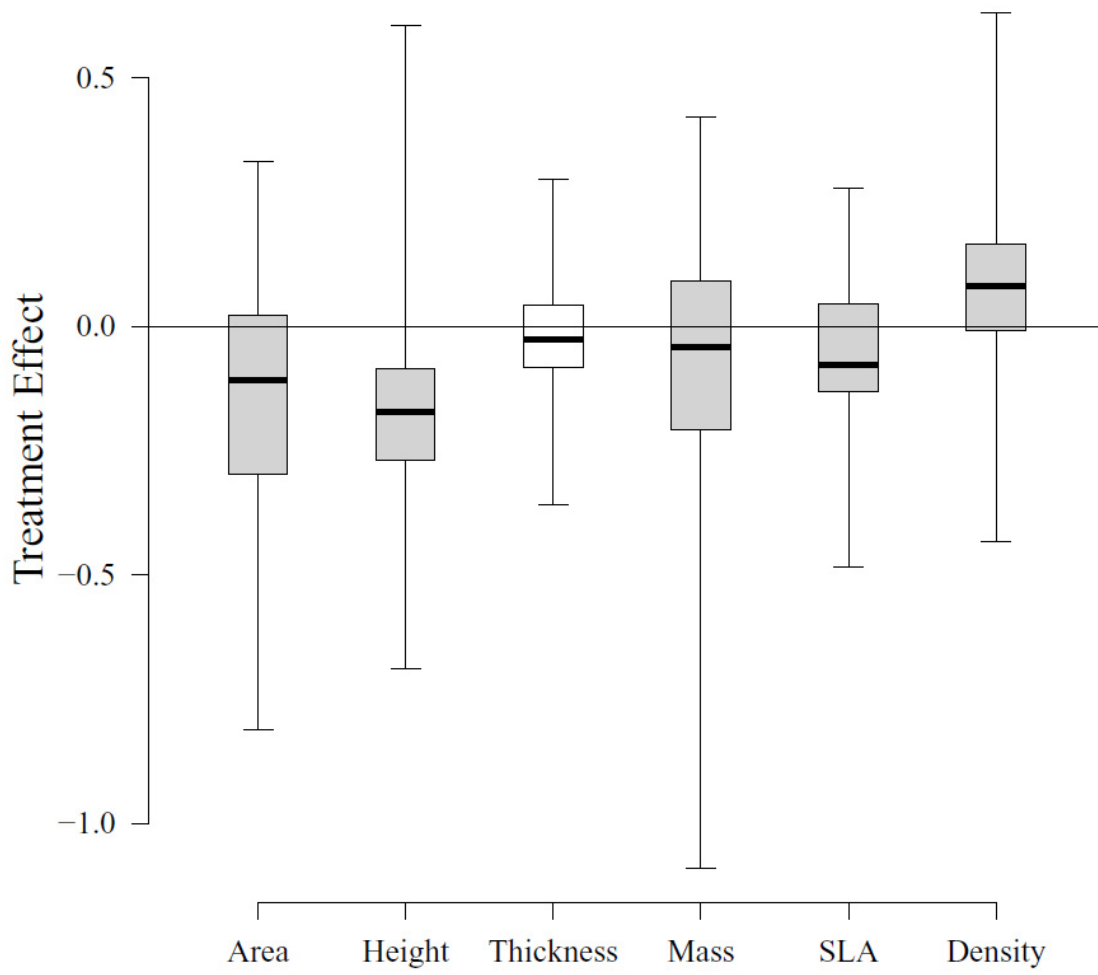


Figure 5

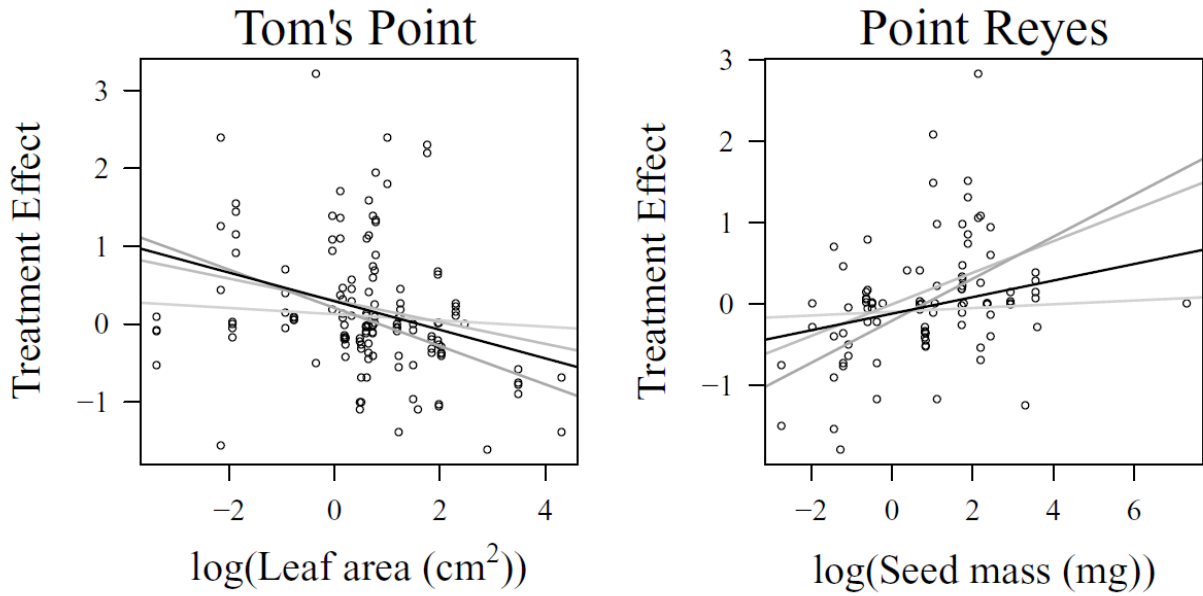


Figure 6

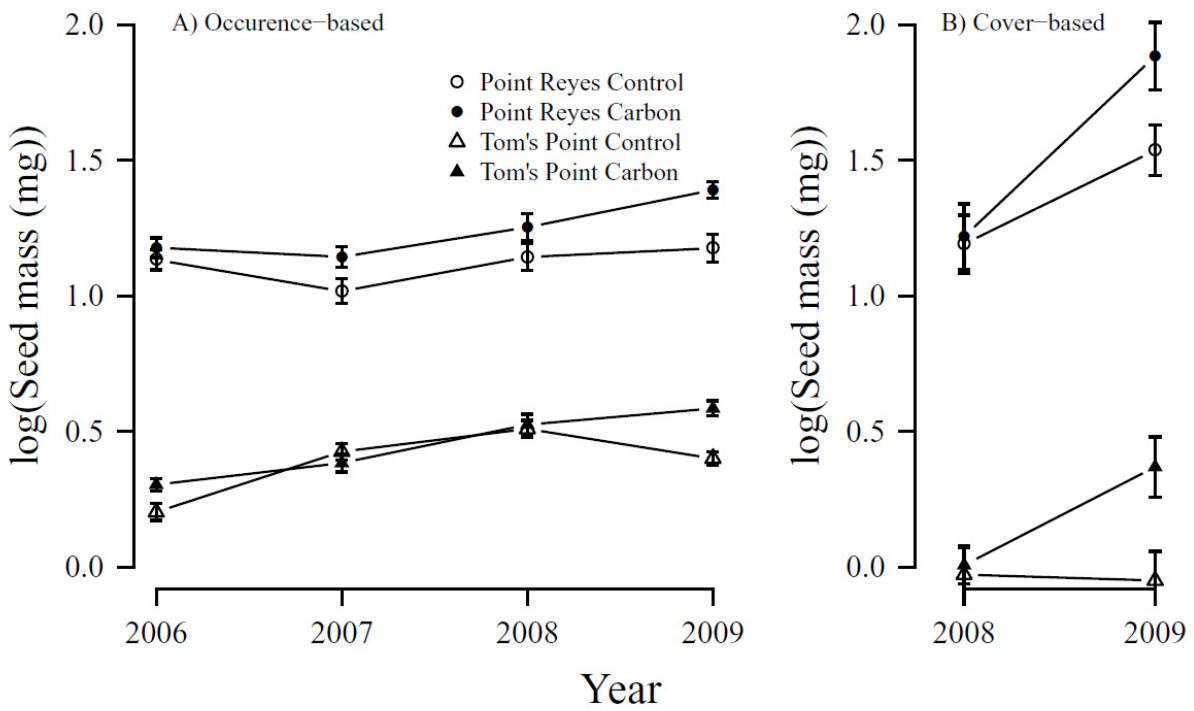


Figure 7

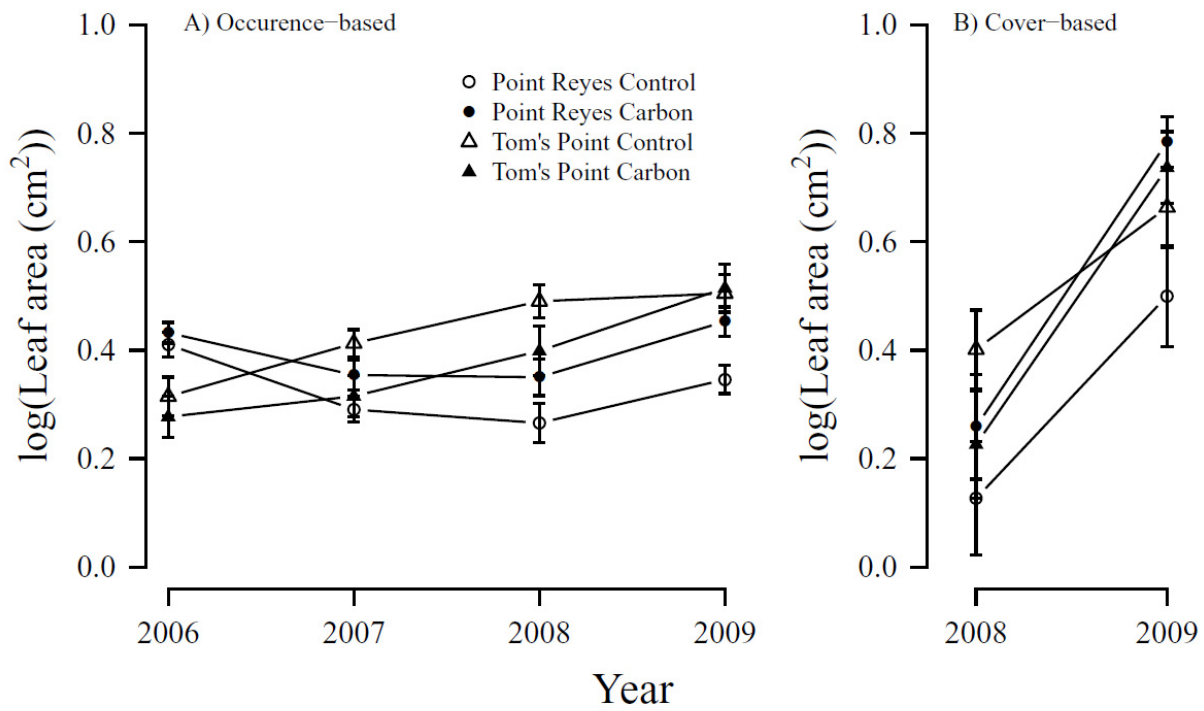


Figure 8

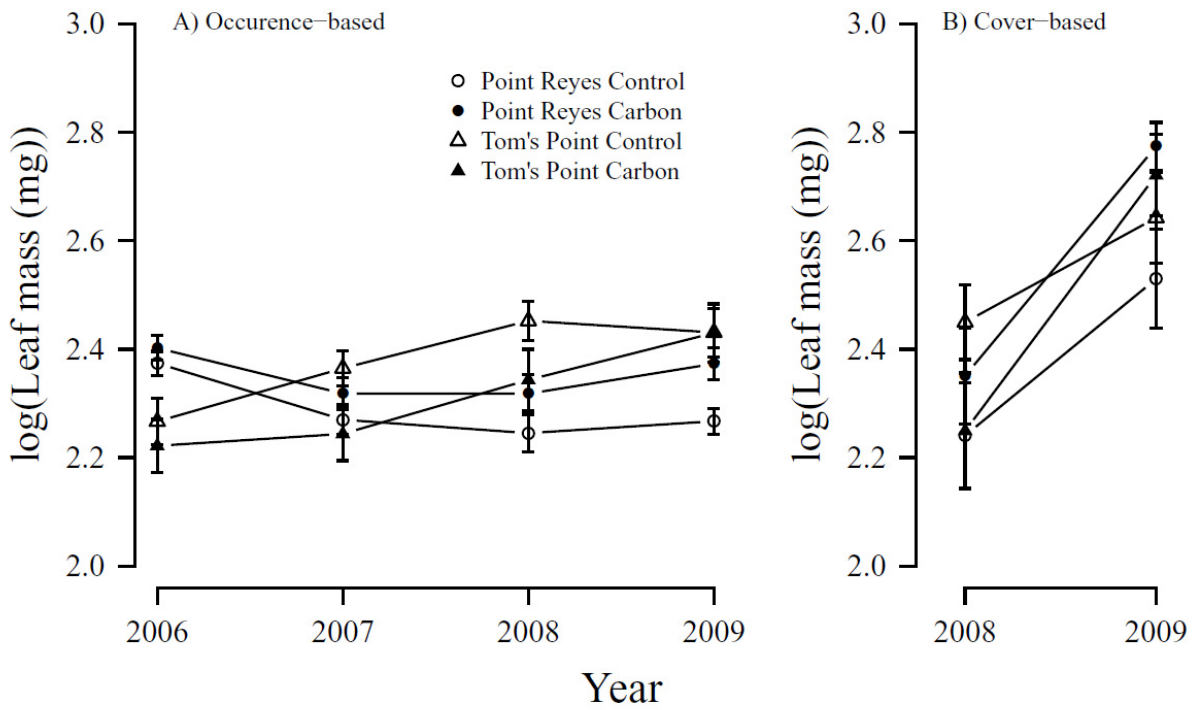


Figure 9

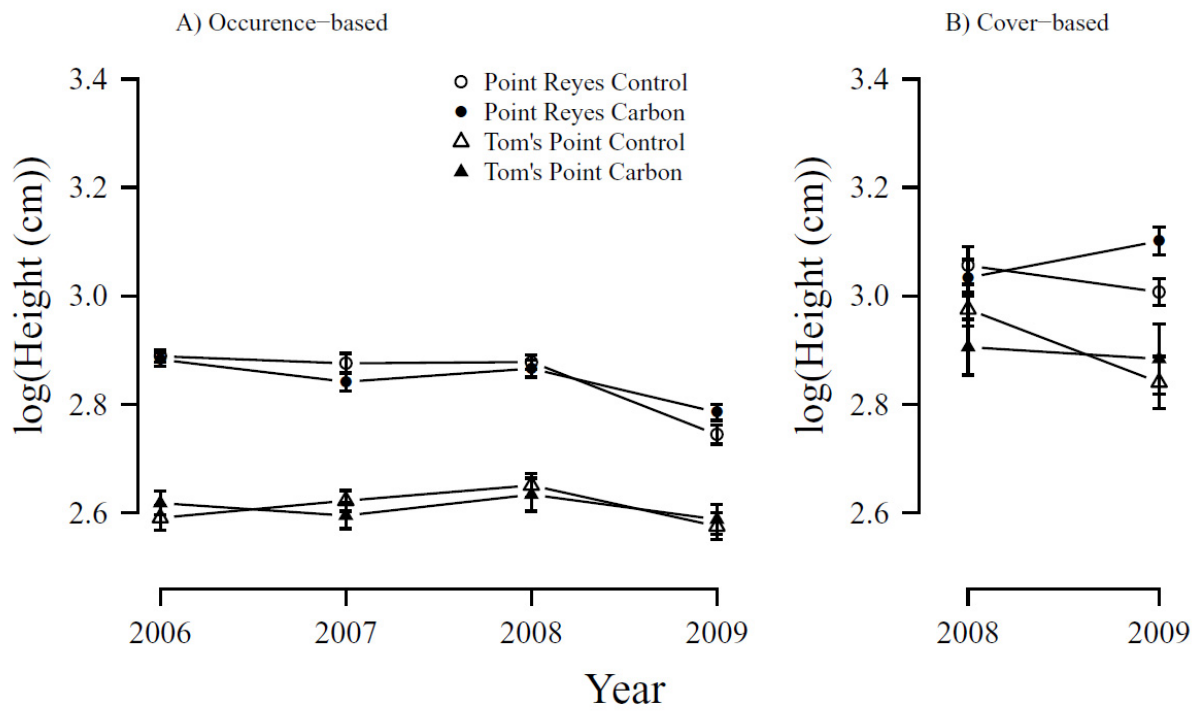


Figure 10

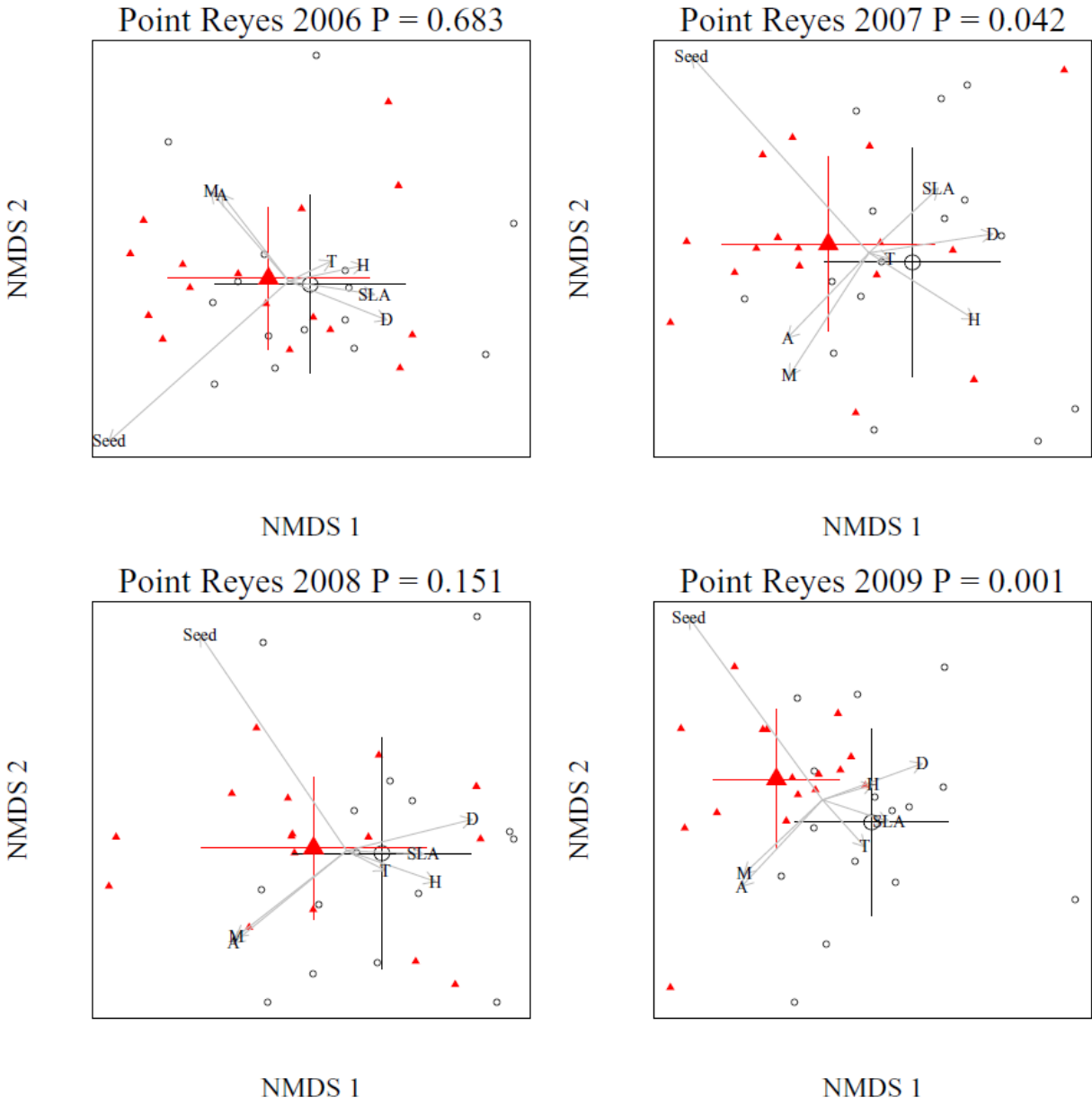


Figure 11

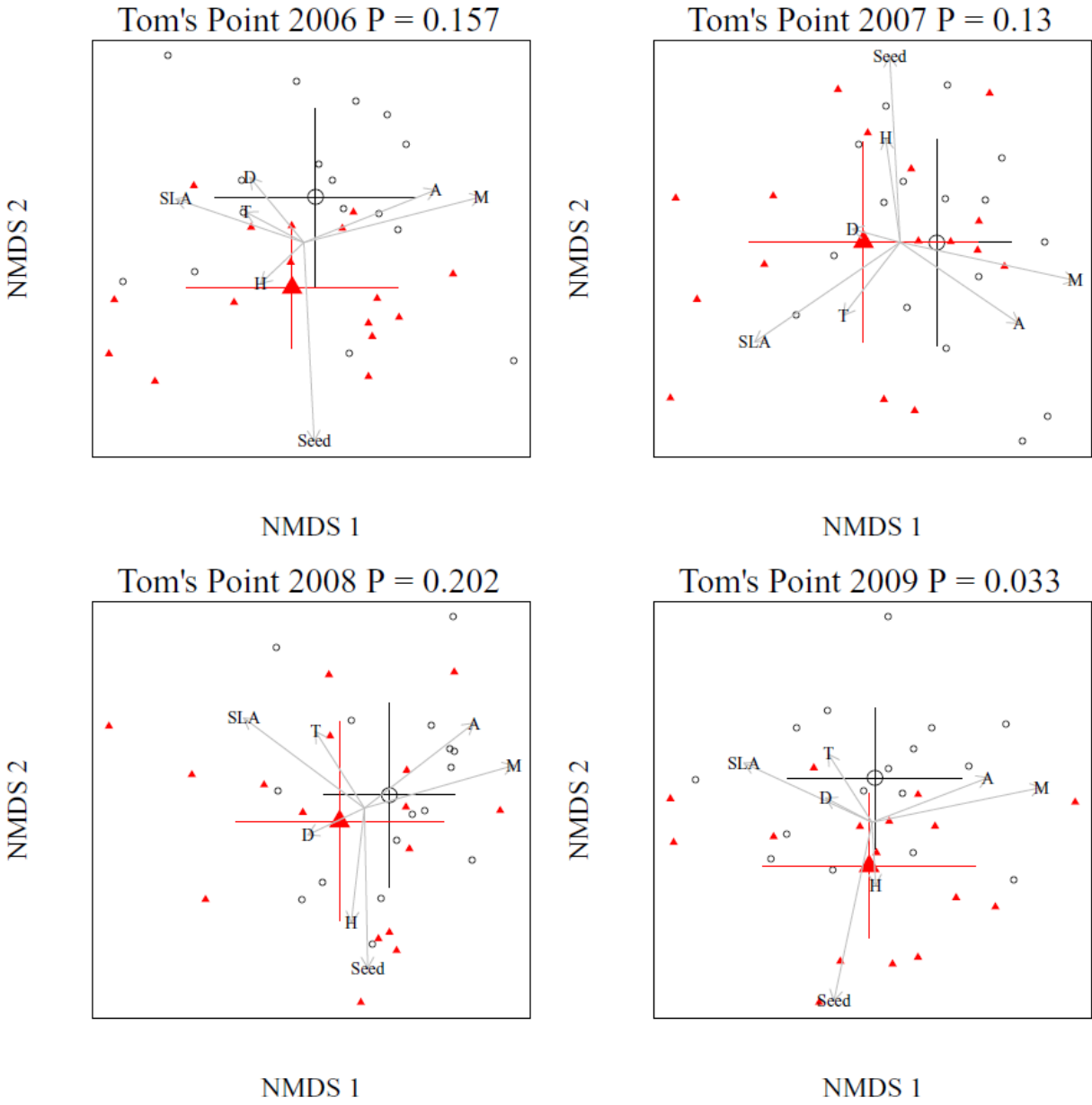


Figure 12

Appendix 1: Summary of species treatment effect sizes and traits. Effect sizes are the mean log occurrence rate in carbon treated plots minus mean log occurrence rate in control plots, across all four years of the experiment. Quantitative traits are the log mean trait value across all measurements of that species (both treatments and both sites). Area refers to leaf area (in log cm^2), height is the height of the highest photosynthetic surface (in log cm), Thick. is the leaf thickness (in log mm), SLA is the specific leaf area (in log cm^2/g) and Dens. is the leaf density (in g/cm^3). N indicates the total number of individuals measured for each species.

Species	Treatment Effect											
	Point Reyes	Tom's Point	Form	Lifespan	Origin	Area	Height	Thick.	Mass	SLA	Dens.	N
<i>Achillea millefolium</i>		-0.39	Forb	Perennial	Native	1.49	2.67	-1.24	4.15	4.25	-0.71	13
<i>Agrostis stolonifera</i>	-1.13		Graminoid	Perennial	Exotic	-0.03	3.74	-1.80	2.67	4.21	-0.11	2
<i>Aira caryophyllea</i>	-0.14	-0.15	Graminoid	Annual	Exotic	-3.38	1.96	-2.59	-1.71	5.24	-0.35	24
<i>Aragallis arvensis</i>	0.17	0.29	Forb	Biennial	Exotic	-0.93	1.75	-1.73	0.31	5.67	-1.64	59
<i>Avena barbata</i>	0.02	2.09	Graminoid	Annual	Exotic	1.00	3.61	-1.55	3.11	4.79	-0.93	25
<i>Baccharis pilularis</i>		-0.57	Shrub	Perennial	Native	0.51	3.23	-1.13	2.82	4.60	-1.17	13
<i>Briza maxima</i>	1.15		Graminoid	Annual	Exotic	0.31	3.43	-1.90	1.92	5.30	-1.09	7
<i>Briza minor</i>		0.63	Graminoid	Annual	Exotic	-2.16	2.16	-2.69	-0.25	5.20	-0.15	3
<i>Bromus carinatus</i>	0.00	0.25	Graminoid	Perennial	Native	1.25	3.48	-1.60	3.62	4.54	-0.64	31
<i>Bromus diandrus</i>	0.00	0.26	Graminoid	Annual	Exotic	0.76	3.37	-1.65	2.81	4.86	-0.90	64
<i>Bromus hordeaceus</i>	-0.47	0.07	Graminoid	Annual	Exotic	-0.77	2.75	-2.03	1.12	5.02	-0.69	60
<i>Carduus pycnocephalus</i>	0.49	-0.58	Forb	Annual	Exotic	1.98	3.26	-0.84	3.95	4.94	-1.79	34
<i>Cirsium vulgare</i>	0.00	-1.04	Forb	Biennial	Exotic	4.31	3.09	-0.49	6.97	4.24	-1.45	1
<i>Claytonia perfoliata</i>			Forb	Annual	Native	0.21	1.96	-0.67	1.45	5.67	-2.69	3
<i>Cynosurus echinatus</i>	0.41		Graminoid	Annual	Exotic	0.72	3.40	-1.97	2.39	5.24	-0.96	4
<i>Danthonia californica</i>		1.13	Graminoid	Perennial	Native	0.11	2.33	-1.52	2.54	4.47	-0.65	9
<i>Daucus pusillus</i>		0.35	Forb	Annual	Native	0.32	2.54	-1.64	2.46	4.77	-0.83	15
<i>Elymus glaucus</i>		-0.28	Graminoid	Perennial	Native	0.64	3.49	-1.65	2.88	4.60	-0.65	26
<i>Erodium botrys</i>	0.24	1.04	Forb	Annual	Exotic	0.65	2.13	-1.67	2.64	4.92	-0.94	46
<i>Eschscholzia californica</i>		1.37	Forb	Perennial	Native	0.78	2.34	-1.60	2.82	4.87	-0.96	15
<i>Festuca arundinacea</i>		2.25	Graminoid	Perennial	Exotic	1.76	3.97	-1.22	4.43	4.23	-0.71	7
<i>Galium aparine</i>		-0.26	Forb	Annual	Native	-2.36	3.22	-2.00	-0.50	5.04	-0.73	1
<i>Geranium dissecta</i>	-0.35		Forb	Annual	Exotic	0.21	1.99	-1.84	1.85	5.27	-1.12	64
<i>Holcus lanatus</i>	-0.35	-0.05	Graminoid	Perennial	Exotic	1.18	3.65	-1.54	3.09	5.00	-1.16	56
<i>Hordeum brachyantherum</i>	0.01		Graminoid	Perennial	Native	0.02	3.41	-2.10	1.83	5.10	-0.70	7
<i>Hordeum murinum</i>	0.02		Graminoid	Annual	Exotic	0.02	3.23	-1.77	1.79	5.14	-1.07	30
<i>Hypochoeris glabra</i>	-0.71	0.27	Forb	Annual	Exotic	1.96	1.28	-1.24	3.35	5.52	-1.98	55
<i>Hypochoeris radicata</i>	0.00	0.19	Forb	Perennial	Exotic	2.30	1.08	-1.05	4.03	5.18	-1.83	31

Appendix 1, part 1

Species	Treatment Effect											
	Point Reyes	Tom's Point	Form	Lifespan	Origin	Area	Height	Thick.	Mass	SLA	Dens.	N
<i>Linum bienne</i>		1.26	Forb	Perennial	Exotic	-1.87	3.22	-2.02	-0.29	5.33	-1.01	5
<i>Lolium perenne</i>	0.08	-0.07	Graminoid	Perennial	Exotic	0.60	3.48	-1.50	2.83	4.70	-0.90	60
<i>Lupinus arboreus</i>	-1.25	-1.10	Forb	Perennial	Native	1.58	3.56	-1.09	4.06	4.43	-1.04	8
<i>Lupinus bicolor</i>	1.95	0.58	Forb	Perennial	Native	0.73	2.69	-1.31	2.80	4.84	-1.22	58
<i>Marah fabaceus</i>	0.00	0.00	Forb	Perennial	Native	2.47	2.85	-1.04	4.29	5.09	-1.75	3
<i>Medicago polymorpha</i>	-0.29		Forb	Annual	Exotic	1.08	2.39	-2.25	2.61	5.38	-1.15	2
<i>Monardella villosa</i>		-0.57	Forb	Perennial	Native	1.22	2.21	-1.43	3.07	5.05	-1.32	3
<i>Oxalis albicans</i>	-0.54	0.25	Forb	Perennial	Native	0.15	1.78	-1.92	1.69	5.37	-1.15	37
<i>Phalaris aquatica</i>			Graminoid	Perennial	Exotic	2.60	4.55	-1.86	4.82	4.69	-0.53	1
<i>Plantago lanceolata</i>		-0.26	Forb	Perennial	Exotic	1.84	1.59	-1.25	3.81	4.94	-1.38	31
<i>Pteridium aquilinum</i>		-0.76	Forb	Perennial	Native	3.48	3.32	-1.08	6.10	4.29	-0.92	26
<i>Ranunculus californicus</i>		-0.63	Forb	Perennial	Native	0.48	2.55	-1.49	2.45	4.94	-1.15	14
<i>Raphanus sativus</i>	0.03		Forb	Biennial	Exotic	2.45	3.47	-1.05	4.57	4.78	-1.43	32
<i>Rubus ursinus</i>	0.00	-0.37	Shrub	Perennial	Native	2.03	2.17	-1.56	4.21	4.73	-0.86	30
<i>Rumex acetosella</i>	0.07	-0.07	Forb	Perennial	Exotic	0.72	2.14	-1.17	2.39	5.24	-1.77	64
Sedge		-0.13	Graminoid			0.18	2.93	-1.84	2.17	4.92	-0.77	31
<i>Silene gallica</i>	-0.40	0.90	Forb	Annual	Exotic	-0.04	3.11	-1.05	1.78	5.08	-1.73	20
<i>Sisyrinchium bellum</i>		0.20	Forb	Perennial	Native	0.61	2.73	-1.40	2.79	4.73	-1.03	8
<i>Sonchus asper</i>	-1.79	-1.61	Forb	Annual	Exotic	2.90	3.28	-1.34	4.07	5.73	-2.09	8
<i>Trifolium microdon</i>		1.35	Forb	Annual	Native	-0.35	1.91	-2.03	1.34	5.21	-0.88	11
<i>Trifolium subterraneum</i>	1.10		Forb	Annual	Exotic	1.43	2.02	-2.05	2.95	5.39	-1.04	16
<i>Vicia hirsuta</i>	0.11		Forb	Annual	Exotic	1.37	3.10	-1.44	3.20	5.08	-1.33	7
<i>Vicia sativa</i>	0.22	0.05	Forb	Annual	Exotic	0.61	2.55	-1.92	2.22	5.30	-1.07	64
<i>Vulpia myuros</i>	-0.01	-0.05	Graminoid	Annual	Exotic	-1.94	2.60	-2.11	0.49	4.49	-0.07	59

Appendix 1, part 2