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Beta diversity gradients of butterflies along productivity axes

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ABSTRACT

Aim. Several lines of evidence suggest that beta diversity, or dissimilarity in species composition, should increase with productivity: (1) the latitudinal species richness gradient is most closely related to productivity and associated latitudinal beta diversity relationships have been described, and (2) the scale dependence of the productivity-diversity relationship implies that there should be a positive productivity-beta diversity relationship. However, such a pattern has not yet been demonstrated at broad scales. We test if there is a gradient of increasing beta diversity with productivity.

Location. Canada.

Methods. Canada was classified into regions of similar productivity regimes along three remotely sensed productivity axes (minimum and integrated annual productivity, seasonality of productivity) and elevation. The overall (β_j), turnover (β_{sim}), and nestedness (β_{nes}) components of beta diversity within each productivity regime were estimated with pairwise dissimilarity metrics, and related to cluster productivity with partial linear regression and with spatial autoregression. Tests were performed for all species, productivity breadth-based subsets (e.g., species occurring in many and a moderate number of productivity regimes), and pre- and post-1970 butterfly records. Beta diversity between adjacent clusters along the productivity gradients was also evaluated.

Results. Within-cluster β_j and β_{sim} increased with productivity and decreased with seasonality. The converse was true for β_{nes} . All species subsets responded similarly, however, productivity-beta diversity relationships were weaker for the post-1970 temporal subset and strongest for species of moderate breadth. Between-cluster beta diversity (β_j) and nestedness (β_{nes}) declined with productivity.

Main conclusions. As predicted, beta diversity of communities within productivity regimes was observed to increase with productivity. This pattern was driven largely by a gradient of species turnover. Therefore, beta diversity may make an important contribution to the broad scale gradient of species richness with productivity. However, this species richness gradient dominates regional beta diversity between productivity regimes, resulting in decreasing between-productivity dissimilarity with productivity driven by a concurrent decline in nestedness.

INTRODUCTION

Patterns of biodiversity have long captured scientific interest. The most widely recognized diversity gradient is the dramatic decrease in species richness from the tropics to the poles, which has been documented many times and is remarkably consistent across taxa (Willig *et al.*, 2003; Hillebrand, 2004). Latitude is merely a proxy of the underlying drivers of biodiversity, which remain unexplained (or, perhaps, over-explained). Numerous competing, non-mutually-exclusive hypotheses have been proposed (Willig *et al.*, 2003). All proposed variables, to some degree and in some situations, correlate with both latitude and diversity (Evans *et al.*, 2005). The hypothesis that has received the strongest support is that the latitudinal diversity gradient is determined by productivity and/or ambient energy (Hawkins *et al.*, 2003; Field *et al.*, 2009).

Beta diversity, or the degree to which local communities are differentiated (Whittaker, 1972), is critical to observed diversity gradients, although its role is relatively poorly understood.

Both the latitudinal diversity gradient and the productivity-diversity relationship are scale dependent, indicating that beta diversity contributes to these richness gradients. The latitudinal diversity gradient is strongest at coarser scales (Hillebrand, 2004), implying that beta diversity declines with latitude. Research on the latitudinal diversity gradient has historically emphasized species richness, but this focus has recently been expanded to beta diversity, with mixed results depending upon the method used to calculate beta (Koleff *et al.*, 2003) and scale of the study (Lennon *et al.*, 2001). In general, however, the expected negative relationship of beta diversity with latitude has been observed, for example, for plants (Qian & Ricklefs 2007; Qian 2008, 2009), birds (Blackburn & Gaston, 1996), mammals (Stevens & Willig, 2002; Rodriguez & Arita, 2004; Qian *et al.*, 2009), caterpillars (Dyer *et al.*, 2007), freshwater animals (Hof *et al.*, 2008), and in cross-taxa meta-analyses at fine scales (Soininen *et al.*, 2007a). Exceptions to this pattern have been birds, when taking into account longitudinal autocorrelation (Gaston *et al.*, 2007), marsupials (Willig & Gannon, 1997), bats (Rodriguez & Arita, 2004), and in cross-taxa meta-analyses at coarse scales (Soininen *et al.*, 2007b).

In contrast to the latitudinal diversity gradient, the productivity-diversity relationship exhibits several forms: monotonically increasing, decreasing, or hump shaped (Waide *et al.*, 1999). This variety of responses may be scale-dependent, as has been demonstrated with lake fauna (Chase & Leibold, 2002; Chase & Ryberg, 2004; Gardezi & Gonzales, 2008). These studies show that the relationship between regional richness and productivity is strong and positive, while richness at the lake scale may be unimodal. Beta diversity (between pond dissimilarity) must increase with productivity to reconcile low local richness yet high regional richness at high productivities. A positive productivity-beta diversity relationship has also been observed for plants on serpentine soils in California (Harrison *et al.*, 2006), but not for birds over larger extents (Bonn *et al.*, 2004; Gaston *et al.*, 2007). However, there are few analyses of broad scale productivity-beta diversity relationships. Most studies of environmental drivers of beta diversity are conducted at relatively small extents or relate beta diversity (distance in species space) to variability or distance in environmental space (e.g., Buckley & Jetz, 2008; Melo *et al.*, 2009), which is a fundamentally different question than whether beta diversity changes systematically with productivity. The latter is the third layer of abstraction in Tuomisto & Ruokolainen's (2006) framework clarifying the "analyzing or explaining beta diversity" debate (Legendre *et al.*, 2005).

Most studies on large scale diversity patterns use range map data. However, this assumes that species have 100% occupancy of their ranges, thereby overestimating local diversity and underestimating beta diversity (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Lira-Noriega *et al.*, 2007). Range maps only support analyses at resolutions of 1-2° or greater (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Lira-Noriega *et al.*, 2007), which may be problematic for conservation planning. Because of within grid cell species turnover, coarse scale diversity estimates may not accurately reflect diversity patterns at the scale of reserve planning, resulting in suboptimal reserve placement (Stevens & Willig, 2002). It is therefore important to characterize diversity components and gradients at fine scales (Shriner *et al.*, 2006). While these resolutions are not supported by range map data, biological specimens and museum collections may provide such an opportunity (Graham *et al.*, 2004). A caveat is that analyses of fine-scaled primary biodiversity data will be more subject to sampling effects, especially incomplete sampling and variable sampling intensity. The impact of sampling effects on estimates of beta diversity are complex (Colwell & Coddington, 1994); beta diversity will be overestimated if rare species are sampled at a portion of the sites where they occur but underestimated if only common

species are sampled. Overestimation of beta diversity is believed to be more common (Chao *et al.*, 2005).

Given that there is a relatively consistent negative latitudinal gradient of beta diversity and that the accompanying latitudinal gradient of species richness is closely related to productivity, we expect there to be a positive productivity-beta diversity relationship. Likewise, this is predicted by the scale-dependence of the productivity-diversity relationship. The goal of this study is to characterize patterns of beta diversity across productivity gradients in Canada. We do so using a national butterfly dataset and remotely sensed measures of productivity.

METHODS

Butterfly data

Butterfly data were obtained from the Canadian Biodiversity Information Facility (<http://www.cbif.gc.ca/>). This dataset synthesizes georeferenced butterfly specimens and observations from 42 collections, published as part of the Canadian contribution to the Global Biodiversity Information Facility (GBIF) primary data network. It contains nearly 200,000 records of approximately 300 species (taxonomy follows Layberry *et al.*, 1998) at 10,000 sites collected from the mid-1800s to the present. Sample sites are unevenly distributed across Canada. Sample intensity, as estimated with Thiessen polygons delineated around sample points (Schulman *et al.*, 2007), spans several orders of magnitude, ranging from 1 km² in southern Canada to 100,520 km² in the Northern Arctic. Median polygon size is 101 km² (mean \pm s.d.: 884 \pm 3930 km²).

We conducted our analyses at the resolution of the sample point, allowing us to characterize beta diversity at a much finer resolution than most broad scale studies, yet still over a large extent. We acknowledge that analyses of primary data will tend to overestimate dissimilarity and will suffer from increased noise, reducing the strength of observed relationships. To reduce the impact of sampling effects upon our conclusions, we excluded points that contained below average species richness for a given productivity level (productivity levels are described below), leaving 2742 points for analyses. Overall, mean species richness was 6.2 spp. pt⁻¹ in the full dataset and 15.9 spp. pt⁻¹ in the subset analyzed.

Productivity data

Productivity data were the Dynamic Habitat Index (DHI) developed by Coops *et al.* (2008) for Canada. The DHI contains three components: minimum and integrated annual productivity, and seasonality of productivity, plus elevation. The first three were derived from the MODIS (Moderate-resolution Imaging Spectroradiometer) fPAR (fraction of absorbed photosynthetically active radiation) product at 1 km resolution (Myneni *et al.*, 2002). DHI components were calculated for each pixel, each year (2000-2005) as the minimum, sum, and coefficient of variation of monthly fPAR, and averaged over the six year time series (Coops *et al.*, 2008, 2009). Elevation data (shuttle radar topography mission, Rabus *et al.*, 2003) were re-expressed as z-scores.

Canada's terrestrial land area was classified into generalized productivity regimes (Coops *et al.*, 2009) along these four layers by the automated two-step multivariate classification in SPSS (Zhang *et al.*, 1997). Two-step is an agglomerative hierarchical clustering algorithm that classifies records according to the distances between them in feature space (i.e., the coordinate space defined by the environmental variables). Performing clustering in two steps greatly increases efficiency for addressing large problems (Zhang *et al.*, 1997), such as clustering the nearly 10 million 1-km² pixels of Canada's land area into productivity regimes. The first step

generates a cluster feature tree to quickly identify pre-clusters. At each branching of the tree, records go to the node to which they are the closest in feature space. At the bottom of the tree, records are either classified into a terminal node, or, if the distance criterion is not satisfied, form a new terminal node. In the second step, a standard hierarchical agglomerative classification (analogous to the unweighted arithmetic average clustering (UPGMA) method familiar in community ecology; Legendre & Legendre, 1998) is applied, treating the pre-clusters as individual cases (Zhang *et al.*, 1997). For this study, 100 pre-clusters were generated using the log-likelihood distance measure, and hierarchically grouped to a 40 cluster resolution (Coops *et al.*, 2009). The resulting DHI clusters identify regions with similar productivity regimes along three productivity variables as well as elevation, rather than a simple partitioning of a single variable into the same number of levels. Productivity of the clusters is expressed with their centroid within DHI space (e.g., the within-cluster mean of the four input variables). We performed all analyses on both the 100 and 40 cluster resolutions. Results were similar at both resolutions, so we present only those of the 40 cluster analyses, which conformed more readily with the regression assumptions.

Beta diversity metrics

We calculated overall beta diversity using the Jaccard index, which is a measure of the pair-wise dissimilarity between two sites:

$$\beta_j = \frac{b + c}{a + b + c},$$

where b and c are the number of species unique to each site and a is the number of shared species. β_j is thus the proportion of species that are not shared between two sites.

However, there are two components of beta diversity that are integrated into broad-sense beta diversity metrics such as β_j : nestedness along a biodiversity gradient (i.e., species present at species poor sites are a subset of those at species rich sites) and species turnover, as measured with a narrow-sense beta diversity metric (Koleff *et al.*, 2003). Simpson's index of beta diversity (Lennon *et al.*, 2001) controls for richness differences between sites and is thus a narrow-sense beta diversity metric, emphasizing species turnover,

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}.$$

β_{sim} calculates the proportion of species in the species poor site that are unique to that site. Baselga (2010) suggests that the nestedness component of beta diversity can be estimated by subtracting beta diversity due to turnover from overall beta diversity, e.g., $\beta_{nes} = \beta_j - \beta_{sim}$. All analyses were performed for each of these three beta diversity metrics. β_j and β_{sim} were calculated in R (R Core Development Team, <http://r-project.org>), with functions in the add-on package vegan (Oksanen *et al.*, 2008).

Within-cluster analyses

Beta diversity is influenced by a number of factors, including the geographic and environmental distances between sample points and, the subject of the current study, the position of sample points along environmental gradients (e.g., productivity). Spatial dependence can influence interpretations in two ways. (1) If spatial dispersion of sample points differs between clusters, apparent differences in within-cluster beta diversity may be due solely to spatial effects. Because there is spatial autocorrelation of community composition, beta diversity generally increases with the geographic separation between points (Nekola & White, 1999). Therefore, a cluster containing densely aggregated butterfly records is expected to exhibit lower beta diversity than one containing only widely dispersed records, independent of their respective productivities.

(2) There may be spatial autocorrelation in beta diversity itself, which is one level of abstraction higher than the autocorrelation of community composition in the previous case. For example, a semivariogram for community composition may plot a dissimilarity metric against lag distance, while a semivariogram for beta diversity would plot the difference in the dissimilarity metric against lag distance. Two analyses, partial regression and spatial autoregressive models, were used to relate within-cluster beta diversity to productivity while addressing each of these levels of autocorrelation.

Partial regression analyses tested if the beta diversity levels of each productivity regime varied with productivity after controlling for differences in geographic and environmental dispersion. Data were prepared for this test by (1) standardizing productivity, elevation, and geographic coordinates by their Canada-wide mean to facilitate intercomparisons of regression coefficients; (2) calculating species composition dissimilarities (β_j , β_{sim} , and β_{nes}), productivity and elevation distances, and Euclidean geographic distances between all sample point pairs, irrespective of cluster membership; and (3) arcsine transforming beta diversity estimates which, as they are expressed as proportion dissimilarity, are bounded by 0 and 1. Multiple regression on distance matrices (MRM; R package *ecodist*, Goslee & Urban, 2008) was used to remove the effects of geographic and environmental distance on beta diversity. Beta diversity between all point pairs (e.g., $n = 3,533,811$ pairwise dissimilarities for the entire species set) was modeled as a function of geographic, productivity, and elevation distance and the residuals from these models were used for further analyses. For each cluster, residual beta diversities from the previous step were averaged for all within-cluster point-pairs. The effect of absolute productivity on beta diversity was tested by relating the cluster mean residual beta diversity to the mean productivity level of that cluster. Each productivity metric was tested individually with single linear regression.

The above partial regression models aggregated corrected dissimilarity estimates to the cluster level. At the point level, generalized least squares (GLS) models with a spatially autocorrelated error term (Pinheiro & Bates, 2000; R package *nlme*, Pinheiro *et al.*, 2009) were performed to test if the uniqueness of the butterfly community at a focal point (relative to points in the same productivity regime) depends upon productivity. The average dissimilarity (β_j , β_{sim} , or β_{nes}) between each point and its cluster-mates was calculated and arcsine transformed. Dissimilarities were modeled as a multivariate function of the standardized productivity variables (because minimum and integrated annual fPAR were highly correlated, the former was excluded from models) and elevation at each point. Spatial autocorrelation of the error terms was modeled with an exponential semivariogram using the geographic coordinates of each sample point and grouping observations by cluster (i.e. the semivariogram considered only within-cluster point pairs). In order to reduce effects of the spatial dispersion of points on beta diversity estimates, focal-point dissimilarities were calculated only for point pairs within three specific distance buffers: within 100 km of the focal point, 450-550 km or 950-1050 km away from the focal point. Buffers were relatively narrow, to isolate the effects of productivity from the effects of space, but wide enough to include a reasonable sample size of cluster-mates separated by the specified distances. Buffer distances are arbitrary, but conform to those used in a previous beta diversity study (Buckley & Jetz, 2008), and were selected to balance distances large enough to capture differences in the distance decay of similarity (based on dissimilarity at a fixed distance, rather than the slope of the distance decay relationship), yet not so large as to sample only point pairs with 100% dissimilarity or to geometrically restrict pairwise

comparisons to points on the periphery of Canada. Analyses were performed separately for each of the buffers.

All measures of within-cluster beta diversity were calculated for the entire species set, as well as for species with broad or moderate productivity niches, as estimated by the number of DHI clusters (at the 100 cluster resolution) at which each species was present. Breadth classes were defined using the 0.33 and 0.66 quantiles of cluster incidences. Moderately broad species ($n=103$) were sampled in 10 to 36 clusters each and, collectively, were found at 3911 points within 98 DHI clusters (1183 sites when considering only points with above cluster average richness of moderately broad species). Broadly distributed species ($n=109$) occurred in more than 36 clusters each (maximum = 90 clusters) and 98 clusters overall, collectively occupying 8947 sites (2616 sites with above cluster average broad species richness).

Between-cluster analyses

Between-cluster beta diversity (β_j , β_{sim} , and β_{nes}) was calculated for cluster pairs that are adjacent in productivity space. Clusters, rather than sample points, were the units of this analysis, so all butterfly records were aggregated to the cluster level. Because cluster order and thus the identities of adjacent clusters differed along the four DHI axes, clusters were reordered and calculations repeated for each productivity metric individually. Between-cluster estimates of beta diversity (arcsine transformed) were related to each DHI axis (using the value of the lower-productivity cluster from the adjacent cluster pair) separately with linear regression.

Temporal turnover

The temporal mismatch between butterfly records (1864-2006) and productivity variables (2000-2005) presents a possible cause for concern. Temporal turnover in butterfly communities may confound our conclusions. To investigate if temporal change in butterfly communities has occurred, partial canonical correspondence analyses (pCCA; ter Braak, 1986; Borcard *et al.*, 1992) were performed on butterfly samples aggregated into cluster-decade units ($n = 439$), with the categorical cluster and decade IDs as explanatory variables. Inclusion of clusters and decades as explanatory variables was determined by forward/backward stepwise variable selection for the CCA models on cluster and decade independently. pCCAs were performed in the R package *vegan* (Oksanen *et al.*, 2008).

RESULTS

Temporal turnover

Clusters and decades alone explained, respectively, 21.7% (rank = 29 dummy variables; Akaike Information Criterion, AIC = 2347.9) and 2.0% (rank = 4 dummy variables; AIC = 2396.1) of the variation in butterfly community composition of cluster-decade aggregates. Decades were largely independent of clusters (i.e., the effect of time was not due to more or different clusters being sampled over time). After partialing out the effects of cluster, decade continued to explain 1.8% of the variation in community composition ($p < 0.005$). In particular, the four most recent decades (1970-2000s) were significantly different from those prior; CCA axis 1 (explaining 0.8% of the variation, and 44% of the variation attributable to decade; $F = 4.1619$, $p < 0.005$) primarily separated these two time periods (pre- and post-1970; not shown). Axis 2 (explaining 0.5% of the total variation and providing 27% of the explanatory power of decade; $F = 2.5622$, $p < 0.005$) separated these four decades, in chronological order. As there was observable change in butterfly communities at the cluster level, all of the within-cluster analyses were repeated splitting the butterfly records into 1864-1969 and 1970-2006 (henceforth: pre- and post-1970) subsets. Although absolute productivity levels are not expected to be

constant between the 2000-2005 MODIS series and, in particular, the pre-1970 time period (e.g., Pouliot *et al.*, 2009), the relative ranking of productivity regimes are assumed to be similar. Nevertheless, changes in community composition were slight (only ~2% of the variation), so results from the entire time period of collections are probably little influenced by temporal shifts.

Within-cluster beta diversity

One quarter of all point pairs shared no species (14% of within-cluster point pairs) and pairwise beta diversities between sampled points were relatively high. Matrix regressions of dissimilarities between all points indicated that butterfly communities are structured both spatially and by productivity (Figure 1, Table 1). Geographic and productivity distances generally explained about 20% of the variation (40% for the moderately broad species set) in β_j and β_{sim} ; these values were slightly lower for β_{nes} . Geographic distance dominated the models of beta diversity, consistently receiving the highest standardized coefficients in the multivariate regression models. The amounts of variation explained by geographic distance alone (Figure 1) were only a few percent lower than those in the multivariate models including both geographic and productivity distance (Table 1). β_j and β_{sim} increased with distance in both geographic and productivity space; β_{nes} showed the opposite pattern. Results were similar across all species and temporal subsets (Table 1).

The residuals from these matrix regression models were used as an estimate of within-cluster beta diversity corrected for spatial, productivity, and elevation distances, and were tested against the three productivity variables (Table 2; productivity relationships from the entire species set plotted in Figure 2). It was necessary to square the cluster-mean residuals of β_j and β_{sim} in order to meet assumptions when modeling them as a function of minimum annual productivity for all species and temporal subsets, as a function of seasonality for the moderately broad and pre1970 subsets, and as a function of elevation for the broad and pre1970 subsets. Both the overall and turnover components of beta diversity of a productivity regime increased with its productivity level (particularly when expressed as mean annual productivity, but also as minimum annual productivity in the case of the pre1970 set) and decreased with seasonality. In contrast, nestedness decreased with integrated annual productivity and increased with seasonality. Patterns were consistent across all species and temporal subsets, although relationships were weaker and nonsignificant in the post1970 set.

Similar patterns were observed in the GLS models of focal point beta diversity with spatially autocorrelated error terms, although R^2 values were lower due to the greater noisiness of observations at the point level (Table 3). A variety of transformations of the beta metrics were necessary to meet assumptions (Table 3). The strongest and most consistent relationship was with integrated annual fPAR. Overall beta diversity and turnover increased with integrated annual productivity and generally decreased with seasonality; nestedness decreased with integrated annual productivity. Relationships of the beta diversity components with elevation depended upon the subsets tested; β_j and β_{sim} decreased with elevation for the entire dataset and the post1970 records, but increased with elevation for the moderately broad species set and the pre1970 records. The reverse was true for β_{nes} . The strength of relationships depended on buffer distance. Productivity was generally unrelated to beta diversity calculated within a 100 km neighborhood, but patterns emerged when considering dissimilarities between the focal point and those 500 km and 1000 km distant.

Between-cluster beta diversity

Aggregating butterfly records to the cluster level reduced pairwise dissimilarities. To meet statistical assumptions, β_j and β_{sim} were squared for models with minimum annual

productivity. Observed patterns were present for β_j , but not β_{sim} , and were the reverse of within-cluster productivity-beta diversity relationships (Figure 3). Overall beta diversity between adjacent (in productivity space) DHI clusters declined with minimum and integrated annual productivity, and modestly with elevation. In contrast to the within-cluster comparisons, the nestedness component of beta diversity varied in the same direction as overall beta diversity, declining with both minimum and integrated annual productivity (Figure 3). There were no relationships with seasonality (Figure 3).

DISCUSSION

Within-cluster beta diversities support the hypothesis that beta diversity increases with productivity, although observed correlations were relatively weak (Figure 2, Tables 2 & 3). Minimum and integrated annual fPAR estimate productivity directly, and both showed the expected positive relationship with beta diversity consistently across metrics (β_j and β_{sim}) and analyses. Conversely, the stability of productivity and length of the growing season decline with increasing seasonality. Likewise, beta diversity was lower in regions of high seasonality. Nestedness declined with absolute productivity and increased with its seasonality. These results contrast with those of previous studies addressing variation of beta diversity, i.e., Tuomisto and Ruokolainen's (2006) third level of abstraction (Bonn *et al.*, 2004; Gaston *et al.*, 2007). However, the geographic extents (southern Africa and global) and thus productivity ranges of these studies are very different from ours. Canada may be an ideal area for detecting large scale productivity-beta diversity gradients, which may be strongest at low productivities. Analogously, Kerr and Packer (1997) found the productivity-species richness relationship to hold true only at the low productivities typical of Canada, but not over the broader range of North American productivities.

The different analyses presented here help reveal some of the controls of the productivity-beta diversity relationship. Beta diversity is the result of three main processes: In the broad sense (e.g., β_j), beta diversity patterns compound underlying species richness gradients and species turnover. Narrow sense beta diversity, or species turnover independent of richness patterns, occurs through either environmental or geographic dispersion of sites. Either variation in the environmental conditions present and the environmental tolerances of the species involved prevent identical butterfly communities from occurring across sites, or geographic distance and dispersal limitation prevent all species from reaching all sites. The present study has shown that, in addition to species richness gradients, environmental filters, and dispersal limitation, beta diversity may also be influenced by the productivity level of the communities compared. On top of these abiotic influences on beta diversity, observed patterns are related to species and taxa traits (e.g., range). As did Gaston *et al.* (2007), we found that beta diversity patterns of the entire species set paralleled those of broadly distributed species. In contrast, species with more restricted productivity niches exhibited stronger productivity-beta diversity relationships, but were able to strengthen the overall pattern relative to beta diversity gradients of broad species only slightly. We tested a single taxon (butterflies), and other taxonomic groups may reveal contrasting patterns. Buckley and Jetz (2008) observed much greater turnover in amphibians, due to more restricted ranges and reduced vagility, than in birds, although spatial patterns of turnover were comparable between both groups.

For Canadian butterfly communities, β_j and β_{sim} , which are broad-sense and narrow-sense beta diversity metrics, respectively, present similar patterns with productivity. Furthermore, these patterns were not reinforced by β_{nes} , which varied in the opposite direction. Nestedness

does not contribute to regional relative to local diversity as, in a perfectly nested system, all of a region's species occur at the most species-rich site. Observed beta diversity-productivity relationships are therefore due, at least in part, to gradients in species turnover within productivity levels. Consequently, greater community diversity at high productivities may amplify the broad scale productivity-diversity gradient. In comparison, local species richness, especially of high diversity sites, seems to be relatively more important to regional richness at low productivities, where beta diversity is lower overall and the contribution of nestedness to beta diversity is greater. Additional work is encouraged to confirm the generality of these patterns, or qualify under which conditions and in which taxa they are expected to occur.

Space is fundamental to beta diversity, and was the dominant factor explaining community dissimilarity in matrix regression models (Table 1). Consequently, the effects of space must be corrected for when estimating beta diversity, either by partialing out space and using residuals for further analysis, or by restricting dissimilarity calculations to narrow distance buffers. Interestingly, beta diversity-productivity relationships were weakest within a 100 km neighborhood of the focal point. This may be a sampling artifact. Because of the haphazard distribution of the butterfly samples, different sets of productivity regimes were included at each buffer distance (e.g., Table 3, "n clusters" column). However, the included clusters were largely the same between the 100 km and 500 km buffer analyses and, for all of the buffer distances, the ranges of productivity values covered were similar. Alternatively, effects of buffer distance may be due to the scale of variation of community composition. In ongoing work with this dataset, we have found that butterfly community composition varies at a scale of several hundred kilometers (Andrew *et al.*, in press). Space has the dominant influence on community composition and beta diversity (Table 1), but its effects are strongest at small separations (e.g., similarity declines exponentially with space; Nekola & White, 1999). Effects of other variables may be most apparent when beta diversity is considered beyond the distances at which spatial effects such as dispersal, metapopulation processes, or source/sink dynamics, are strong. This is noteworthy because most focal-cell type analyses of beta diversity investigate only dissimilarity from the immediate neighborhood (e.g., Gaston *et al.*, 2007; and, although not a focal-cell analysis, Bonn *et al.*, 2004), suggesting that previous reports of negative or no relationships between these variables may simply be due to the chosen neighborhood. Neighborhood sizes should thus be determined carefully with consideration of the spatial scale of community composition, rather than simply the grid resolution of the input biodiversity or environmental data. Put another way, if differences in beta diversity are due to variation in the distance decay of similarity (Nekola & White, 1999) but are not reflected in initial similarities, they will only be captured if analyses are performed with separation distances large enough for such differences to manifest. Therefore, it is valuable to repeat analyses computing dissimilarity from a variety of distance rings, or to extract multiple parameters from the distance decay relationship, such as the slope (e.g., Qian & Ricklefs, 2007; Buckley & Jetz, 2008; Qian 2008, 2009; Qian *et al.*, 2009), the initial similarity (the intercept or value at the first distance class; Soininen *et al.*, 2007b), and the distance to half-similarity (Soininen *et al.*, 2007b), as the response variable.

The presence of a beta diversity-productivity gradient when controlling for species richness and space may be caused by greater environmental heterogeneity at higher productivities; this is a subject for further study. Environmental heterogeneity includes habitat diversity, resource diversity, etc.; the former has a strong, positive relationship with butterfly biodiversity in Canada (Kerr *et al.*, 2001). There have been few tests if environmental heterogeneity increases with productivity, and support for this premise is limited. Chase &

Leibold (2002) showed that between-pond heterogeneity was unrelated to watershed productivity, and could not explain the observed productivity-beta diversity relationship. Harrison *et al.* (2006) observed increasing variability of habitat features with productivity at the plot scale, but this did not affect beta diversity. Plant biodiversity (i.e., resource diversity for butterflies), is positively associated with productivity, leading to correlations between plant and butterfly diversity. However, path analyses revealed that this correlation is due to a shared underlying variable (productivity) (Hawkins & Porter, 2003). Although a direct link between plant richness and butterfly richness was not supported, beta diversity was not explicitly tested as a mechanism for such a link (Hawkins & Porter, 2003). Alternatives to the environmental heterogeneity hypothesis are that greater beta diversity at high productivities may be maintained by alternate stable states (Chase & Liebold, 2002) or cyclical community assembly (Steiner & Liebold, 2004). Another possibility is that communities at low productivity, in particular, have not yet reached equilibrium following the last glaciation, and are characterized by generalists with high dispersal capacity (e.g., Qian & Ricklefs, 2007), resulting in reduced between-community dissimilarity.

Beta diversity was originally proposed to document species turnover and community changes over specific environmental gradients (Whittaker, 1972). Our between-cluster analyses considered such turnover between successive points on productivity gradients. Community changes along the productivity gradient were gradual; beta diversities tended to be moderate between adjacent clusters, without abrupt shifts in community composition. However, dissimilarity between adjacent productivity regimes increased at low productivities. This between-productivity regime beta diversity gradient is most likely the result of an underlying species richness gradient, as suggested by the similar slopes and strengths of correlations of productivity with the overall and nestedness components of beta diversity, and the lack of a correlation with the turnover component. There is a known butterfly richness-productivity gradient in Canada: For example, we found a correlation of $R^2 = 0.35$ between overall cluster richness and integrated annual productivity (not shown) and such a gradient has been demonstrated elsewhere for Canadian butterflies (Kerr *et al.*, 2001).

Finally, beta diversity-productivity relationships appear to be changing over time, and, especially, to have diminished over recent decades. Differences between the pre- and post-1970 time periods may be partly due to sampling effects. Butterfly collections were more extensive (i.e., over more sites) but less intensive (i.e., fewer individuals and species per site) post 1970. Nevertheless, butterfly species are clearly responding to climate change, both in Canada (Kharouba *et al.*, 2009) and elsewhere (Hickling *et al.*, 2006; Parmesan *et al.*, 1999), which is expected to affect community composition. White and Kerr (2007) report homogenization (i.e., a reduction in beta diversity) of butterfly communities in human-dominated areas in Canada. Since these are concentrated in the southern, more productive portion of the country, such a homogenization could reduce the strength of beta diversity-productivity relationships. Conversely, the beta diversity gradient may be weakening due to productivity changes at the low end of the gradient (which is where climate change to date has been most extreme; Serreze *et al.*, 2000). These possibilities are suggestive and warrant further investigation.

CONCLUSIONS

There are several lines of evidence that suggest that beta diversity, or the dissimilarity in species composition between sites, should increase with productivity. However, this has not yet been demonstrated in broad-scale, macroecological studies. Here we show that beta diversity of

Canadian butterfly communities is positively related to productivity. At low productivities, butterfly communities are less dissimilar and the contribution of nestedness to dissimilarity is more important; turnover between butterfly communities increases with productivity. Therefore, a positive productivity-beta diversity gradient reinforces the broad scale productivity-richness relationship. In contrast, due to the productivity-species richness relationship, dissimilarity between productivity regimes along the productivity gradient was greatest at low productivity.

Our estimates of species dissimilarity are generally high and the strength of the observed beta diversity-productivity relationships are generally low, which are presumably due to data quality (especially variable sampling effort) and the decision to analyze primary survey data, rather than gridding the butterfly data to a coarser resolution or interpolating distribution models from the survey points. However, despite the noise, it is important to conduct biodiversity analyses at fine scales, as these are the scales of conservation planning (Shriner *et al.*, 2006). Reserve network design and placement should be informed by beta diversity to maximize the number of species protected (e.g., Wiersma & Urban, 2005). Our results indicate that, given the greater dissimilarity and greater contribution of turnover to dissimilarity of local communities at high productivity, more or larger reserves may be necessary to conserve butterfly biodiversity in such regions. This is especially true as, like butterfly biodiversity, human population density is also concentrated in the most productive regions (Luck, 2007). It may not be necessary to represent all productivity regimes in a reserve network: at high productivities between-productivity beta diversity is relatively low while at low productivities, between-productivity differences are driven by nestedness and the underlying species richness gradient.

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REFERENCES

- Andrew, M.E., Wulder, M.A., & Coops, N.C. (*in press*). How do butterflies define ecosystems? A comparison of ecological regionalization schemes. *Biological Conservation*, doi:10.1016/j.biocon.2011.01.010.
- Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134-143.
- Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos*, **77**, 146-152.
- Bonn, A., Storch, D., & Gaston, K.J. (2004) Structure of the species-energy relationship. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 1685-1691.
- Borcard, D., Legendre, P., & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045-1055.
- Buckley, L.B. & Jetz, W. (2008) Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17836-17841.
- Chao, A., Chazdon, R.L., Colwell, R.K., & Shen, T.J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148-159.
- Chase, J.M. & Leibold, M.A. (2002) Spatial scale dictates the productivity-biodiversity relationship. *Nature*, **416**, 427-430.
- Chase, J.M. & Ryberg, W.A. (2004) connectivity, scale-dependence, and the productivity-diversity relationship. *Ecology Letters*, **7**, 676-683.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **345**, 101-118.
- Coops, N. C., Wulder, M. A., Duro, D. C., Han, T., & Berry, S. (2008) The development of a Canadian dynamic habitat index using multi-temporal satellite estimates of canopy light absorbance. *Ecological Indicators*, **8**, 754-766.
- Coops, N. C., Wulder, M. A., & Iwanicka, D. (2009) An environmental domain classification of Canada using earth observation data for biodiversity assessment. *Ecological Informatics*, **4**, 8-22.
- Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A., & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696-700.
- Evans, K.L., Warren, P.H., & Gaston, K.J. (2005) Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1-25.
- Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., & Turner,

- J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132-147.
- Gardezi, T. & Gonzalez, A. (2008) Scale dependence of species-energy relationships: evidence from fishes in thousands of lakes. *American Naturalist*, **171**, 800-815.
- Gaston, K.J., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T.S., Rasmussen, P.C., Lennon, J.J., Bennett, P.M., Owens, I.P.F., & Blackburn, T.M. (2007) Spatial turnover in the global avifauna. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 1567-1574.
- Goslee, S. & Urban, D. (2008) *ecodist: Dissimilarity-based functions for ecological analysis*. Available online (accessed January 19, 2010): <http://cran.r-project.org/>.
- Graham, C.H., Ferrier, S., Huettman, F., Moritz, C., & Peterson, A.T. (2004) New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*, **19**, 497-503.
- Harrison, S., Davies, K.F., Safford, H.D., & Viers, J.H. (2006) Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology*, **94**, 110-117.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.
- Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist*, **161**, 40-49.
- Hickling, R., Roy, D. B., Hill, J.K., Fox, R., & Thomas, C.D. (2006) the distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450-455.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192-211.
- Hof, C., Brändle, M., & Brandl, R. (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. *Global Ecology and Biogeography*, **17**, 539-546.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 13384-13389.
- Hurlbert, A.H. & White, E.P. (2005) Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters*, **8**, 319-327.
- Kerr, J. T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature*, **385**, 252-254.
- Kerr, J.T., Southwood, T.R.E., & Cihlar, J. (2001) Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Sciences*, **98**, 11365-11370.

- Kharouba, H.M., Algar, A.C., & Kerr, J.T. (2009) historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment. *Ecology*, **90**, 2213-2222.
- Koleff, P., Lennon, J.J., & Gaston, K.J. (2003) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography*, **12**, 483-498.
- Layberry, R.A., Hall, P.W., & Lafontaine, J.D. (1998) *The Butterflies of Canada*. University of Toronto Press, Toronto.
- Legendre, P. & Legendre, L. (1998) *Numerical Ecology*, 2 edn. Elsevier, Amsterdam.
- Legendre, P., Borcard, D., & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435-450.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D., & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966-979.
- Lira-Noriega, A., Soberón, J., Navarro-Sigüenza, A.G., Nakazawa, Y., & Peterson, A.T. (2007) Scale dependency of diversity components estimated from primary biodiversity data and distribution maps. *Diversity and Distributions*, **13**, 185-195.
- Luck, G.W. (2007) The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography*, **34**, 201-212.
- Melo, A.S., Rangel, T.F.L.V.B., & Diniz-Filho, J.A.F. (2009) Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, **32**, 226-236.
- Myneni, R.B., Hoffman, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, A., Friedl, M., Morisette, J.T., Votava, P., Nemani, R.R., & Running, S.W. (2002) Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment*, **83**, 214-231.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867-878.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. (2008) *vegan: Community ecology package*. Available online (accessed April 17, 2009): <http://cran.r-project.org/>.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., & Warren, M. (1999) poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579-583.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer Verlag, New York.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2009) *nlme: Linear and nonlinear mixed effects models*. Available online (accessed January 18, 2010): <http://cran.r-project.org/>.
- Pouliot, D., Latifovic, R., & Olthof, I. (2009) Trends in vegetation NDVI from 1 km AVHRR data over Canada for the period 1985-2006. *International Journal of Remote Sensing*, **30**, 149-168.

- Qian, H. (2008) A latitudinal gradient of beta diversity for exotic vascular plant species in North America. *Diversity and Distributions*, **14**, 556-560.
- Qian, H. (2009) Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, **18**, 327-332.
- Qian, H. & Ricklefs, R.E. (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. *Ecology Letters*, **10**, 737-744.
- Qian, H., Badgley, C., & Fox, D.L. (2009) The latitudinal gradient of beta diversity in relation to climate and topography for mammals in North America. *Global Ecology and Biogeography*, **18**, 111-122.
- Rabus, B., Eineder, M., Roth, A., & Bamler, R. (2003) The Shuttle Radar Topography Mission - a New Class of Digital Elevation Models Acquired by Spaceborne Radar. *ISPRS Journal of Photogrammetry and Remote Sensing*, **57**, 241-262.
- Rodríguez, P. & Arita, H.T. (2004) Beta diversity and latitude in North American mammals: testing the hypothesis of covariation. *Ecography*, **27**, 547-556.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Schulman, L., Toivonen, T., & Ruokolainen, K. (2007) Analysing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography*, **34**, 1388-1399.
- Serreze, M.C., Walsh, J.E., Chapin III, F.S., Osterkamp, T., Dyrgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T., & Barry, G. (2000) Observational evidence of recent change in the northern high-latitude environment. *Climate Change*, **46**, 159-207.
- Shriner, S.A., Wilson, K.R., & Flather, C.H. (2006) Reserve networks based on richness hotspots and representation vary with scale. *Ecological Applications*, **16**, 1660-1673.
- Soininen, J., Lennon, J.J., & Hillebrand, H. (2007a) A multivariate analysis of beta diversity across organisms and environments. *Ecology*, **88**, 2830-2838.
- Soininen, J., McDonald, R., & Hillebrand, H. (2007b) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3-12.
- Steiner, C.F. & Leibold, M.A. (2004) Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology*, **85**, 107-113.
- Stevens, R.D. & Willig, M.R. (2002) Geographical ecology at the community level: perspectives on the diversity of New World bats. *Ecology*, **83**, 545-560.
- ter Braak, C.J.F. (1986) canonical correspondence-analysis - a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167-1179.
- Tuomisto, H. & Ruokolainen, K. (2006) Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology*, **87**, 2697-2708.
- Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257-300.

- White, P.J.T. & Kerr, J.T. (2007) Human impacts on environment-diversity relationships: evidence for biotic homogenization from butterfly species richness patterns. *Global Ecology and Biogeography*, **16**, 290-299.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213-251.
- Wiersma, Y.F. & Urban, D.L. (2005) Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology*, **19**, 1262-1272.
- Willig, M.R. & Gannon, M.R. (1997) Gradients of species density and turnover in marsupials: a hemispheric perspective. *Journal of Mammalogy*, **78**, 756-765.
- Willig, M.R., Kaufman, D.M., & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics*, **34**, 273-309.
- Zhang, T.R.R.L.M. (1997) BIRCH: A new data clustering algorithm and its applications. *Data Mining and Knowledge Discovery*, **1**, 141-182.

BIOSKETCH

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Table 1. Slopes and significance tests of multivariate matrix regression models relating dissimilarity in butterfly species composition (calculated with either Jaccard's or Simpson's distance measure, and, representing nestedness, the difference between the two) to geographic and environmental (in dynamic habitat index productivity space; fPAR = fraction of absorbed photosynthetically active radiation) distances. Analyses were performed for the entire species set, productivity breadth-based subsets of the butterfly records (broad and moderate) and temporal subsets of the butterfly records (pre-1970 and post-1970). Significant relationships are highlighted with • ($p < 0.1$), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

	Jaccard		Simpson		nestedness	
All species						
geographic distance	0.0499	***	0.0888	***	-0.0622	***
min fPAR distance	-0.0074	***	-0.0119	***	0.0079	***
integrated fPAR distance	0.0102	***	0.0143	***	-0.0078	***
fPAR seasonality distance	0.0306	***	0.0550	***	-0.0434	***
elevation distance	0.0211	***	0.0370	***	-0.0258	***
F	210800	***	190500	***	151300	***
R2	0.2297		0.2123		0.1763	
Broadly distributed species						
geographic distance	0.0502	***	0.0878	***	-0.0577	***
min fPAR distance	-0.0091	***	-0.0141	***	0.0086	***
integrated fPAR distance	0.0066	***	0.0079	**	-0.0028	•
fPAR seasonality distance	0.0393	***	0.0683	***	-0.0510	***
elevation distance	0.0237	***	0.0396	***	-0.0254	***
F	175600	***	155100	***	116800	***
R2	0.2043		0.1849		0.1459	
Moderately distributed species						
geographic distance	0.0891	***	0.1536	***	-0.1058	***
min fPAR distance	-0.0047	***	-0.0077	***	0.0056	***
integrated fPAR distance	0.0236	***	0.0352	***	-0.0212	***
fPAR seasonality distance	-0.0220	***	-0.0343	***	0.0202	***
elevation distance	0.0369	***	0.0642	***	-0.0457	***
F	94170	***	85560	***	82030	***
R2	0.4024		0.3796		0.3697	
Pre-1970 records						
geographic distance	0.0437	***	0.0815	***	-0.0602	***
min fPAR distance	0.0017	***	-0.0012	***	0.0017	*
integrated fPAR distance	0.0080	***	0.0072	***	-0.0029	***
fPAR seasonality distance	0.0252	***	0.0516	***	-0.0420	***
elevation distance	0.0194	***	0.0352	***	-0.0260	***
F	13500	***	12120	***	10130	***
R2	0.1744		0.1594		0.1368	
Post-1970 records						
geographic distance	0.0517	***	0.0907	***	-0.0627	***
min fPAR distance	-0.0091	***	-0.0156	***	0.0108	***
integrated fPAR distance	0.0134	***	0.0225	***	-0.0137	***
fPAR seasonality distance	0.0265	***	0.0479	***	-0.0386	***
elevation distance	0.0214	***	0.0372	***	-0.0254	***
F	134800	***	123900	***	98380	***
R2	0.2218		0.2077		0.1722	

Table 2. Slopes and R^2 values of regressions relating productivity variables (fPAR = fraction of absorbed photosynthetically active radiation) to within productivity regime beta diversity corrected for geographic and environmental separation. Analyses were performed for the entire species set, productivity breadth-based subsets of the butterfly records (broad and moderate) and temporal subsets of the butterfly records (pre-1970 and post-1970). Significant relationships are highlighted with \bullet ($p < 0.1$), $*$ ($p < 0.05$), $**$ ($p < 0.01$), and $***$ ($p < 0.001$).

	Jaccard			Simpson			nestedness		
	Slope	R^2		Slope	R^2		Slope	R^2	
All species									
min fPAR	0.0006	0.0522		0.0035	0.0641		-0.0030	0.0763	\bullet
integrated fPAR	0.0017	0.2740	***	0.0034	0.2447	**	-0.0022	0.2327	**
fPAR seasonality	-0.1104	0.2790	***	-0.2289	0.2805	***	0.1503	0.2604	***
elevation	0.0026	0.0030		0.0099	0.0101		-0.0054	0.0065	
Broadly distributed species									
min fPAR	0.0002	0.0083		0.0024	0.0225		-0.0027	0.0419	
integrated fPAR	0.0013	0.1416	*	0.0028	0.1513	*	-0.0022	0.1575	*
fPAR seasonality	-0.0668	0.0973	\bullet	-0.1790	0.1497	*	0.1470	0.1701	**
elevation	0.0001	0.0000		0.0062	0.0039		-0.0082	0.0102	
Moderately distributed species									
min fPAR	0.0015	0.0071		0.0014	0.0014		-0.0012	0.0052	
integrated fPAR	0.0052	0.2939	***	0.0067	0.2485	**	-0.0027	0.1481	*
fPAR seasonality	-0.2187	0.2151	**	-0.3938	0.1599	*	0.1824	0.1691	**
elevation	-0.0035	0.0007		0.0111	0.0033		-0.0292	0.0843	\bullet
Pre-1970 records									
min fPAR	0.0028	0.1998	**	0.0117	0.2091	**	-0.0064	0.1615	*
integrated fPAR	0.0016	0.1008	*	0.0032	0.1146	*	-0.0023	0.1098	*
fPAR seasonality	-0.0423	0.0623		-0.1838	0.0712		0.1355	0.0993	\bullet
elevation	0.0016	0.0017		0.0080	0.0026		-0.0107	0.0120	
Post-1970 records									
min fPAR	0.0000	0.0000		0.0002	0.0001		-0.0010	0.0051	
integrated fPAR	0.0011	0.0464		0.0015	0.0329		-0.0009	0.0252	
fPAR seasonality	-0.0581	0.0328		-0.0759	0.0205		0.0379	0.0110	
elevation	-0.0108	0.0219		-0.0206	0.0292		0.0171	0.0435	

Table 3. Slopes of generalized least squares models with spatially autocorrelated errors, as well as transformations applied to the dependent variable (β_{as} refers to the arcsine transform of the dissimilarity measures), relating productivity variables to mean dissimilarity in butterfly species composition (calculated with either Jaccard's or Simpson's distance measure, and, representing nestedness, the difference between the two) of a focal point to points in the same productivity regime within a specified distance buffer (points within 100 km, points within 450-550 km, and points within 950-1050 km). fPAR is the fraction of absorbed photosynthetically active radiation. Pseudo- R^2 values, taken from simple linear regression models between predicted and observed beta diversities, are also reported. Analyses were performed for the entire species set, productivity breadth-based subsets of the butterfly records (broad and moderate) and temporal subsets of the butterfly records (pre-1970 and post-1970). Significant relationships are highlighted with \bullet ($p < 0.1$), \ast ($p < 0.05$), $\ast\ast$ ($p < 0.01$), and $\ast\ast\ast$ ($p < 0.001$).

	n clusters	n points	Jaccard					Simpson					nestedness				
			transform	integrated fPAR	fPAR seasonality	elevation	R^2	transform	integrated fPAR	fPAR seasonality	elevation	R^2	transform	integrated fPAR	fPAR seasonality	elevation	R^2
All species																	
100km	38	2318	β_{as}	0.0098	0.0117	-0.0072 \bullet	0.0043	β_{as}^2	0.0159	0.0216	-0.0091	0.0049	β_{as}	-0.0019	-0.0027	0.0006	0.0016
500km	36	2610	β_{as}	0.0073 \ast	0.0023	-0.0058 \ast	0.0085	$(\beta_{as}-0.3)^{-0.5\ddagger}$	-0.0073	-0.0055	0.0007	0.0013	$\beta_{as}^{4.5}$	-0.0033	-0.0045	0.0005	0.0036
1000km	26	2252	β_{as}^2	0.0138 \ast	-0.0113	-0.0109	0.0101	β_{as}	0.0103 \bullet	-0.0045	-0.0036	0.0039	β_{as}	-0.0083 \bullet	0.0014	-0.0003	0.0004
Broadly distributed species																	
100km	37	2288	β_{as}	0.0061	0.0047	-0.0013	0.0026	β_{as}	0.0058	0.0038	0.0025	0.0051	β_{as}^4	0.0018	0.0030	-0.0036	0.0001
500km	35	2560	β_{as}	0.0093 \bullet	0.0097 \bullet	-0.0020	0.0047	β_{as}	0.0166	0.0205 \ast	-0.0036	0.0099	β_{as}	-0.0129	-0.0163 \ast	0.0022	0.0130
1000km	28	2241	β_{as}^3	0.0319 \bullet	0.0007	-0.0016	0.0001	β_{as}^2	0.0310 \ast	0.0080	0.0018	0.0036	$\log(\beta_{as})$	-0.0304	-0.0149	0.0017	0.0017
Moderately distributed species																	
100km	36	1012	$\sqrt{\beta_{as}}$	0.0037	-0.0101	0.0053	0.0354	$\beta_{as}^{0.3}$	0.0008	-0.0106	0.0043	0.0422	β_{as}^3	0.0101	0.0143	-0.0187 \ast	0.0117
500km	28	1005	$\beta_{as}^{6.5}$	0.2003 $\ast\ast$	-0.8477 $\ast\ast$	-0.0215	0.0093	$\beta_{as}^{2.75}$	0.0408 \ast	-0.1420 $\ast\ast$	0.0183	0.0333	β_{as}	-0.0091 \ast	0.0291 \ast	-0.0120 \bullet	0.0733
1000km	17	636	$\beta_{as}^{2.5}$	0.0713 $\ast\ast$	-0.0700	0.0621 \ast	0.1161	β_{as}	0.0353 $\ast\ast$	-0.0402	0.0379 $\ast\ast$	0.1139	β_{as}	-0.0240 $\ast\ast$	0.0272	-0.0304 $\ast\ast\ast$	0.1047
Pre-1970 records																	
100km	31	571	β_{as}	0.0159 \ast	0.0044	-0.0008	0.0051	β_{as}	0.0221	0.0110	0.0032	0.0042	β_{as}	-0.0062	-0.0033	-0.0054	0.0001
500km	26	699	β_{as}	0.0175 $\ast\ast\ast$	-0.0097	0.0044	0.0565	β_{as}	0.0275 $\ast\ast$	-0.0131	0.0139 \bullet	0.0553	β_{as}	-0.0187 \ast	0.0068	-0.0130 \ast	0.0526
1000km	22	588	β_{as}	0.0100 \ast	-0.0158	0.0133 $\ast\ast$	0.0415	β_{as}	0.0157 \ast	-0.0287	0.0250 $\ast\ast$	0.0440	β_{as}	-0.0119 \bullet	0.0177	-0.0202 $\ast\ast$	0.0445
Post-1970 records																	
100km	36	1879	$(\beta_{as}-0.5)^{-2\ddagger}$	0.0100	0.0163	0.0799	0.0007	$\log(\beta_{as})$	-0.0123	-0.0281	-0.0039	0.0004	β_{as}^2	0.0038	0.0075	-0.0008	0.0043
500km	35	2108	β_{as}^3	0.0259 \bullet	0.0053	-0.0347 \ast	0.0203	β_{as}^2	0.0185	0.0026	-0.0247 \ast	0.0188	β_{as}	-0.0059	-0.0007	0.0076 \bullet	0.0139
1000km	24	1819	$(\beta_{as}-0.75)^3$	0.0026 \bullet	-0.0098 \bullet	-0.0034	0.0084	β_{as}	0.0056	-0.0041	0.0052	0.0148	β_{as}	-0.0045	0.0014	-0.0061	0.0317

\ddagger Note that this transformation inverts the pattern between productivity and beta diversity.

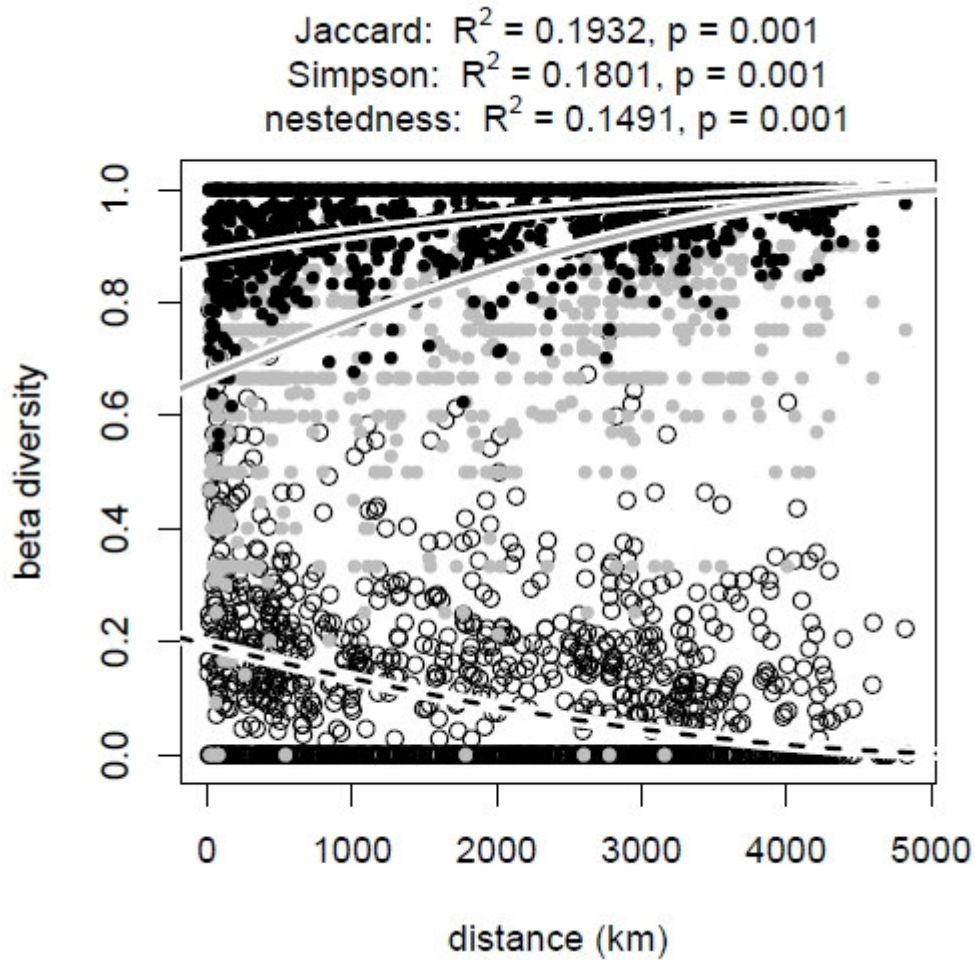


Figure 1. Relationship between geographic distance and the three measures of pairwise beta diversity: Jaccard's distance in black, Simpson's distance in grey, and the nestedness component of beta diversity in open circles. Lines are the matrix regression models fitted on the arcsine transformed beta estimates, and back-transformed to the original variables for these plots. For clarity, only 0.01% of all point-pairs are plotted.

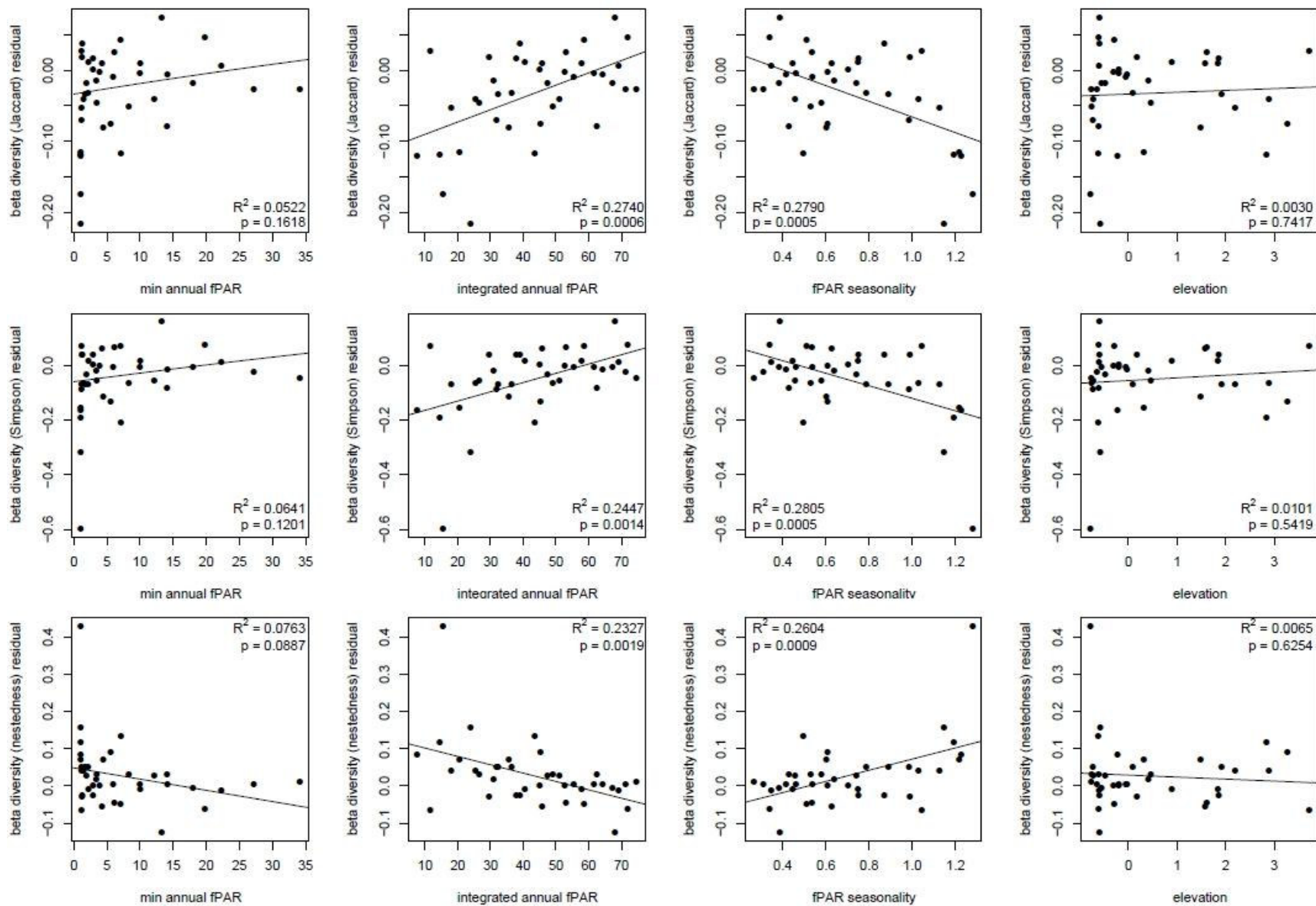


Figure 2. Within-cluster productivity-beta diversity (as corrected for geographic and environmental distance between samples) patterns along the four productivity axes (fPAR = fraction of absorbed photosynthetically active radiation). Beta diversity has been calculated with Jaccard's index in the first row, Simpson's index in the second, and the nestedness component of beta diversity in the third. Results from the entire species set are shown. Fitted lines correspond to the regression models of Table 2.

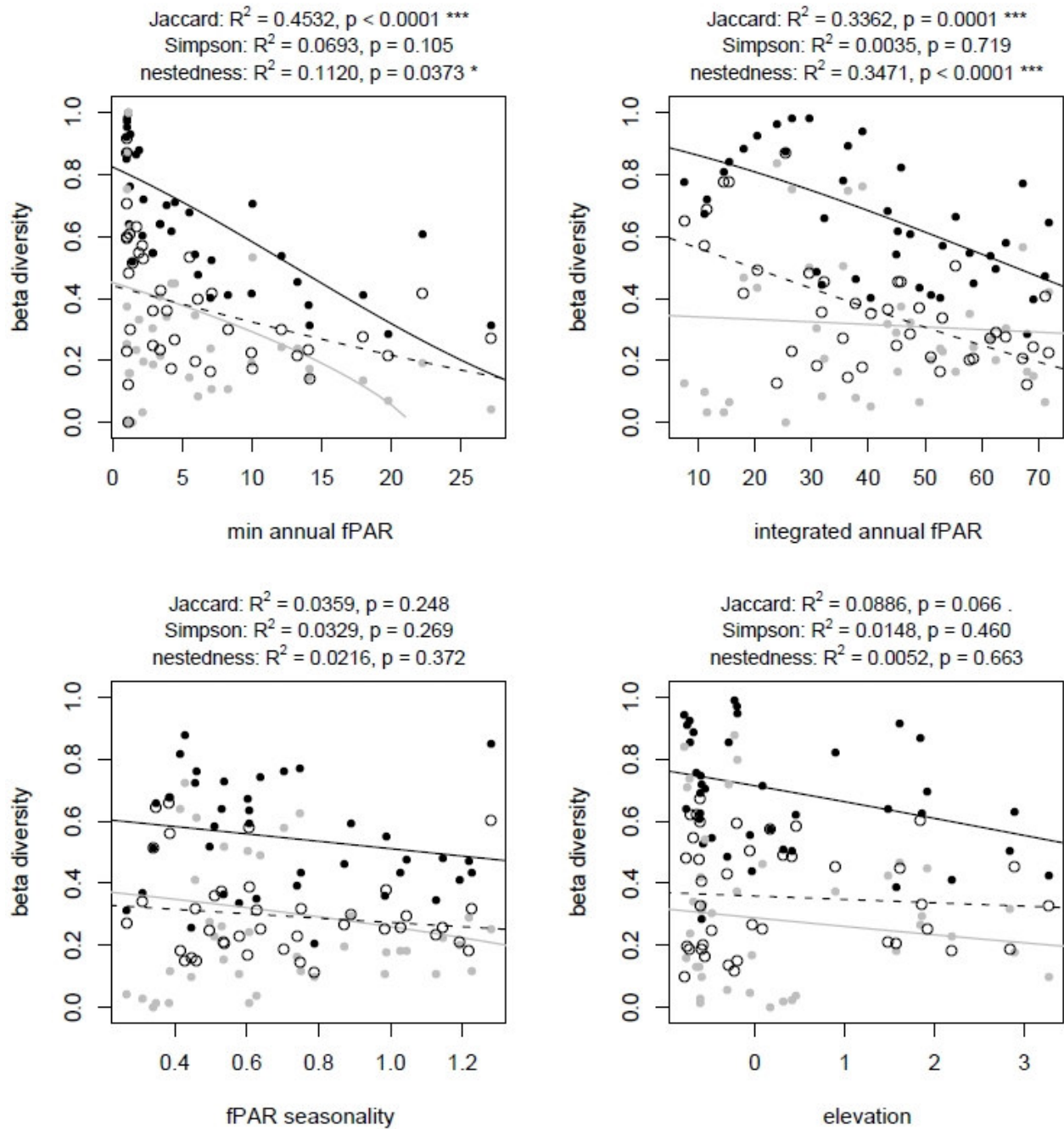


Figure 3. Between adjacent cluster productivity-beta diversity patterns along the four productivity axes (fPAR = fraction of absorbed photosynthetically active radiation). Beta diversity has been calculated with Jaccard's index in black, Simpson's index in grey, and the nestedness component of beta diversity in open circles. Lines are the regression models fitted on the arcsine transformed beta estimates, and back-transformed to the original variables for these plots.