Scale dependence of vegetation–environment relationships: a meta-analysis of multivariate data

Andrew Siefert, Catherine Ravenscroft, David Althoff, Juan C. Alvarez-Yépiz, Benjamin E. Carter, Kelsey L. Glennon, J. Mason Heberling, In Su Jo, Alyssa Pontes, Amy Sauer, Adam Willis & Jason D. Fridley

Siefert, A. (Corresponding author, asiefert@syr.edu), **Ravenscroft, C.** (chravens@syr.edu), **Althoff, D.** (dmalthof@syr.edu), **Carter, B.E.** (becarter@syr.edu), **Glennon, K.L.** (klglennon@gmail.com), **Heberling, J.M.** (jmheberl@syr.edu), **Jo, I.S.** (ijo@syr.edu), **Pontes, A.** (awpontes@syr.edu), **Sauer, A.** (aksauer@syr.edu), **Willis, A.** (adwillis@syr.edu) & **Fridley, J.D.** (fridley@syr.edu): Department of Biology, Syracuse University, 107 College Place, Syracuse, NY, 13244, USA

Alvarez-Yépiz, J.C. (jualvare@syr.edu): College of Environmental Science and Forestry, State University of New York, One Forestry Drive, Syracuse, NY, 13210, USA

Abstract

Questions: How does spatial scale (extent and grain) influence the relative importance of different environmental factors as determinants of plant community composition? Are there general scale thresholds that mark the transition from primarily edaphic to primarily climatic control of plant communities?

Location: Global.

Methods: We surveyed the empirical literature and identified 89 analyses from 63 published studies that analysed vegetation–environment relationships involving at least two categories of predictor variables (edaphic, climatic, topographic, biotic, spatial or disturbance-related). For each analysis, we identified the primary predictor variable (i.e. the variable that explained the most variation in community composition) and the relative effect size of the best predictor variable from each category. We defined 'primacy' as the proportion of times a variable category was primary when it was measured, and analysed primacy and the relative effect size of each category as a function of spatial extent and grain. We also analysed the subset of studies that measured both edaphic and climatic variables to identify spatial extent and grain thresholds for the primacy of these factors.

Results: Edaphic variables had the highest primacy in the overall data set and at fine grain sizes (<200 m^2), but there were no strong trends in primacy across studies of varying spatial extent. We detected trends of increasing relative effect size of climatic variables with increasing spatial extent, and decreasing relative effect size of edaphic variables with increasing spatial grain, although these patterns were not statistically significant. Among studies that measured both edaphic and climatic variables, the importance of climate factors relative to edaphic factors increased with increasing spatial extent and grain, with scale thresholds of 1995 km^2 for extent and 295 m^2 for grain.

Conclusions: Our study illustrates that vegetation–environment relationships depend on the spatial scale (extent and grain) of observation and provide empirical support for the view that there is a transition from a primarily edaphic influence to a primarily climatic influence on plant community composition with increasing spatial scale.

Introduction

A central goal of plant community ecology is to identify the processes that drive spatial variation in species composition. Despite evidence that ecological patterns and processes can depend greatly on the spatial scale of observation (Greig-Smith 1952; Allen & Starr 1982; Levin 1992; Reed et al. 1993), vegetation studies are generally conducted at a single scale, so it remains unclear how the relative influence of different environmental factors on community composition varies with spatial scale. There is a long-standing assumption among plant ecologists that

edaphic variables, such as soil chemistry, texture and depth, control community composition at fine scales, whereas climatic variables like temperature and precipitation are most important at broad scales (Warming 1895; Schimper 1903; Kruckeberg 2004; Palmer 2007). However, this notion has surprisingly little direct empirical support, and it is not known at what scale, if any, a transition from a primarily edaphic influence to a primarily climatic influence on vegetation–environment relationships occurs.

Vegetation–environment relationships are typically detected by measuring environmental variables and species composition across multiple sampling units and using multivariate analyses, such as ordination (Kent & Coker 1992) and Mantel tests (Urban et al. 2002) to determine how much between-sample variance in community composition can be explained by between-sample variance in environmental factors. The ability of a study to detect an effect of an environmental factor on species composition is therefore dependent on both the degree to which species differentially respond to the factor and the extent to which the between-sample variance in that factor can be resolved given the spatial scale of the study (Reed et al. 1993). Because environmental factors differ in the spatial scales at which they vary (Burrough 1981), the relative strength of the relationship between different environmental factors and species composition should depend on the spatial scale of the study.

Spatial scale comprises two elements, extent and grain (Turner 2005), both of which may influence the amount of variance observed in a given environmental factor and thus its observed relationship with species composition. Extent is defined as the overall area encompassed by a study, and grain is defined as the area of the smallest unit of observation (Palmer & White 1994). Because most environmental variables are spatially autocorrelated, their variance tends to increase with increasing extent (Wiens 1989;

Palmer 2007), but this relationship depends on the inherent spatial structure of the variable. For many edaphic variables, such as soil pH or nitrogen concentration, high variance occurs at fine spatial scales (Palmer 1990; Lechowicz & Bell 1991), so increasing extent beyond a certain point will result in relatively little added variance (Fig. 1a). Conversely, many climatic variables, such as temperature and precipitation, vary across much broader scales (Bell et al. 1993), so variance will increase considerably with extent up to very broad scales (Fig. 1a). We therefore expect the influence of coarse-grained variables (e.g. climate) on species composition to increase relative to that of fine-grained variables (e.g. edaphic) with increasing spatial extent.

Changing the grain of the study may also influence the amount of observed between-sample variance and therefore the relative effect sizes of different environmental factors. As grain increases, more environmental variance is included within samples and is thus averaged out, decreasing the amount of between-sample variance available to explain variation in species composition (Wiens 1989). This decrease should be strongest in fine-grained variables but negligible in coarse-grained variables (Fig. 1b). Consequently, we expect the influence of coarse-grained variables (e.g. climate) to increase relative to that of fine-grained variables (e.g. edaphic) with increasing spatial grain. For both spatial extent and grain, this suggests there is a scale threshold where edaphic factors give way to climatic factors as the primary determinants of species composition across sample units. Identification of such a threshold, if general, would be of considerable significance in the study and management of vegetation (Palmer 2007).

In this study, we conducted a meta-analysis of vegetation studies to evaluate how spatial scale (extent and grain) influences the relative importance of different environ-
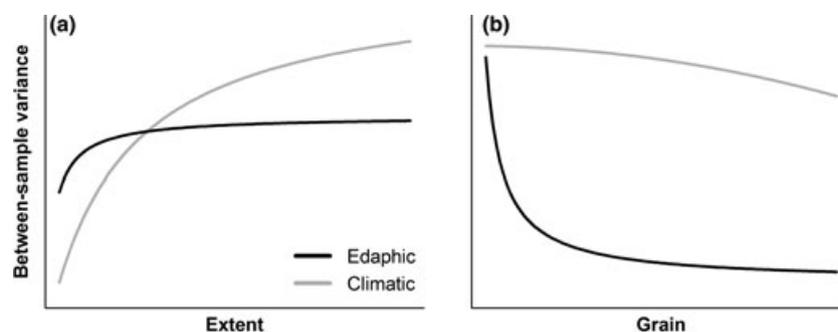
Fig. 1. Theoretical expectations of the amount of between-sample variance in climatic and edaphic factors as a function of spatial extent and grain. (**a**) As extent increases, between-sample variance increases due to spatial autocorrelation of environmental variables. Variance saturates at relatively small extent for edaphic variables, because most variation is found at fine scales, but variance continues to accumulate at relatively broad scales for climatic variables. (**b**) As grain increases, between-sample variance decreases as more variance is included within plots and thus averaged out. The decrease is more rapid for edaphic variables, which exhibit high fine-scale variation, than for climatic variables, which vary over broader scales.

mental factors as determinants of plant community composition. We classified environmental factors into six categories (edaphic, climatic, topographic, disturbance-related, biotic, spatial) and used effect sizes extracted from published studies to determine their relative ability to explain variation in plant community composition across a range of spatial scales. We also conducted a more detailed analysis of our two categories of greatest interest, edaphic and climatic variables (based on Schimper's (1903) 'rules'; Kruckeberg 2004), to determine whether there is a general scale threshold that marks the transition from edaphic to climatic control of plant community composition. We address the difficulties associated with comparing the output of different multivariate analysis methods and suggest guidelines for analysing vegetation–environment relationships and reporting results that would facilitate future meta-analyses.

Methods

Data compilation

We searched the ISI Web of Knowledge database for vegetation–environment studies published in the period 1990–2010 to be included in the meta-analysis. We limited the search to studies using four widely used and supported multivariate data analysis methods: canonical correspondence analysis (CCA), detrended correspondence analysis (DCA), Mantel tests and nonmetric multidimensional scaling (NMDS). We did not include studies using linear ordination methods, such as PCA and RDA, as they have been found to be generally inappropriate for analysis of vegetation data (McCune & Grace 2002). For each publication year, we performed the following topic keyword searches: (1) '(Vegetation OR Plant OR Community) AND (NMS OR NMDS OR MDS)'; (2) '(Vegetation OR Plant OR Community) AND Mantel'; (3) '(Vegetation OR Plant OR Community) AND CCA'; and (4) '(Vegetation OR Plant OR Community) AND DCA'. Additionally, due to the high frequency of pertinent studies in the *Journal of Vegetation Science* and *Journal of Biogeography*, each issue (1990–2010) of these journals was explored individually for topics related to gradient analysis and species composition. Of the 2213 total studies returned from the searches, we determined that 419 studies involved analysis of vegetation–environment relationships. We included in the meta-analysis all studies that (1) reported the spatial extent and grain of the study, or included maps from which these values could be determined and (2) reported effect size statistics for vegetation–environment correlations involving at least two categories of predictor variables (Table 1). Despite the large number of vegetation studies returned from our

Table 1. Classification scheme for predictor variables in vegetation–environment studies. For each category, we provide examples of specific variables measured in studies included in our meta-analysis.

Predictor variable category	Measured variables
Biotic	Canopy cover, canopy type, maximum vegetation height, tree basal area, tree species, NDVI, number of stems, moss cover
Climatic	Annual mean temperature, coldest month temperature, annual mean precipitation, growing season precipitation, summer precipitation, precipitation seasonality, annual mean rainfall, CV of annual rainfall, aridity, evaporation, evapotranspiration, humidity, continentality, degree-days >5 °C, growing season duration, insolation, photosynthetically active radiation
Disturbance	Time since disturbance, land-use intensity, land-use history, fire frequency, fire intensity, erosion, development, distance to village, glaciation, grazing intensity, hurricane damage
Edaphic	Soil texture, bulk density, rock cover, bedrock type, soil nutrient concentrations (e.g. N, P, K, Ca, Al, Mg, Mn, Cu, Zn, Fe, S), nutrient ratios, pH, conductivity, cation exchange capacity, organic matter content, soil depth, horizon depth, litter depth, soil moisture, water level, drainage, fertility
Spatial	Geographic distance, latitude, longitude, region
Topographic	Elevation, elevation range, aspect, exposure, depression, aspect, radiation index, slope, slope position, topography

search, many did not report extent, grain or appropriate effect size statistics. As a result, we included a total of 63 studies (89 separate analyses) in the final meta-analysis (Appendix S1). For the purpose of comparing general groups of predictor variables across studies, we assigned each variable to one of six categories: climatic, edaphic, topographic, disturbance, biotic and spatial factors (Table 1). From selected papers, we only used effect size statistics derived from analyses of 'simple' (using the variable of interest as the only predictor variable) and not 'partial' relationships (using multiple predictor variables) between environmental variables and community composition, because partial correlations depend not only on the relationship between the predictor variable of interest and the response variable, but also on correlations among predictor variables.

Effect sizes

Different multivariate analysis methods produce different effect size statistics, but all reflect the amount of among-sample variation in community composition explained by a given predictor variable. Studies using Mantel tests

reported effect size as Mantel's *r*, which reflects the relationship between dissimilarity matrices for predictor variables and community composition (McCune & Grace 2002). Studies using ordination techniques (CCA, DCA, NMDS) sometimes reported coefficients of determination (r^2) for linear or surface models of predictor variables fit to ordinations of community composition data (Dargie 1984). Other studies using CCA quantified effect sizes as the proportion of total variance in community composition data explained by a given predictor variable, calculated as the ratio of the first eigenvalue of a CCA constrained by the variable of interest and the sum of all eigenvalues (total inertia) of an unconstrained CA of the community composition data (Økland & Eilertsen 1994). Most CCA and DCA studies only reported correlations between environmental variables and individual ordination axes. Because we required a single effect size statistic per variable per study, we developed a new metric, called the 'multivariate effect size statistic' (MESS), which incorporates correlations with multiple ordination axes into a single measure of effect size:

$$MESS = \sum_{i=1}^{N} r_i^2 \lambda_i$$

where N is the number of ordination axes included, r_i is the correlation coefficient for the environmental variable and sample scores on the ith ordination axis, and λ_i is the eigenvalue of the ith axis. MESS is effectively an average of correlation coefficients across multiple ordination axes, weighted by the amount of variance accounted for by each axis. The specifics of the formula are mathematically arbitrary and were chosen to maximize the correlation between MESS and more standard effect size metrics calculated from simulated data sets (see below). We calculated MESS values when possible for studies that did not report effect sizes but otherwise met our criteria.

Because effect size metrics from different multivariate methods or different data sets are not directly comparable (Økland 1999), we used relative rather than absolute effect sizes in our analyses. We calculated relative effect size as the ratio of the effect size of a given variable to the maximum effect size of any variable in the study. Relative effect size therefore measures how well a predictor variable explains variation in community composition relative to other variables measured in the same study. Using relative rather than absolute effect sizes was necessary for analysing trends across data sets, but it has some disadvantages. The relative effect size of a given variable is dependent on the other variables included in a study, potentially complicating detection of trends with respect to spatial scale. Below we describe how we attempted to deal with these issues.

Simulations

We analysed whether MESS accurately reflects correlations between community composition and predictor variables using 1000 simulated data sets of community composition and environmental predictor values generated by a simple niche model (see Appendix S1 for detailed description of simulations). For each simulated data set, we ran a CCA and DCA and calculated standard measures of effect size (proportion of total inertia in CCA explained by an environmental variable and r^2 of environmental vector fit for DCA) and corresponding MESS values for each predictor variable. To determine the sensitivity of the statistic to the number of CCA or DCA axes included, MESS was calculated using either the first two or first four ordination axes. In addition, for CCA we calculated MESS using both inter-set and intra-set correlations, because most studies did not report which were used. Inter-set correlations are correlations between environmental variables and WA scores (derived from the species matrix); intra-set correlations are correlations between environmental variables and LC scores (linear combinations of environmental variables) (Palmer 1993). We calculated the coefficient of determination (r^2) between standard effect size statistics and corresponding MESS values across predictor variables for each simulated data set, repeating the procedure 1000 times to obtain a distribution of coefficients of determination.

Analysis

We analysed the influence of extent and grain on vegetation–environment correlations in two ways. First, we determined how often a particular predictor category (e.g. climatic, edaphic, etc.) was the best predictor in a study across four classes of spatial extent (<1, 1–100, 100–10 000 and >10 000 km^2) and four classes of grain size (<50, 50–200, 200–1000 and >1000 m^2). We called this measure *primacy*, which we defined as the percentage of cases where a given predictor variable category explained the most variance in species composition relative to the total number of studies which analysed a variable of that category (following Field et al. 2009). Primacy gives a general measure of the importance of each category to species composition to allow for comparisons between bin classes, and attempts to correct for any potential biases in the literature, where particular variables could be disproportionately chosen more often for analysis (Field et al. 2009). It was for this reason that we only included studies that analysed more than one category type in our final meta-analysis (i.e. a measured variable better explained species composition patterns relative to other variables of another category).

Second, we performed logistic regressions of relative effect size (0–100%) against extent and grain to examine the abilities of the different predictor variable categories to explain variation in community composition as a continuous function of spatial scale. When a study included more than one variable within a category, we used only the variable with the highest relative effect size within its category. To protect against artefacts induced by variation in the number of predictor variables per category across studies, we used a null model to determine the expected relationships between relative effect size of each variable category and extent and grain under random permutations of effect sizes among variables within studies. We used a randomization procedure to produce 1000 randomized data sets, and then performed logistic regression analyses on each to produce null distributions of slopes for the relationships between relative effect size and extent and grain. By comparing the slopes from the observed data to the null distributions, we were able to determine if the observed relationships could have been generated by random variation. Relative effect size could also be biased by which other predictor variable categories were included in a study (e.g. edaphic variables could have higher relative effect sizes in studies that did not measure topographic variables). To account for this, we created dummy variables indicating whether each predictor variable category was included in a study, and included theme as covariates in logistic regressions. Effects of these dummy variables or their interactions with spatial extent or grain were never statistically significant ($P > 0.25$), so we did not include them in the analyses presented here.

We were also concerned about potential biases arising from different multivariate methods. To test whether multivariate method influenced the results of the meta-analysis, we grouped studies into three categories – direct ordination (CCA), indirect ordination (DCA and NMDS) or Mantel test – and included this as a categorical variable in logistic regressions. Multivariate method did not influence mean relative effect size or its variation with respect to spatial extent or grain in any case ($P > 0.5$), so we did not include it in the final analysis.

Third, because our spatial scaling hypotheses emphasized edaphic and climatic variables, we selected the subset of studies that considered both edaphic and climatic predictor variables ($n = 23$) for further analysis. For each study we subtracted the relative effect of the best climatic variable from that of the best edaphic variable. Values above zero suggest that edaphic factors are more important than climatic factors as determinants of community composition and vice versa. We used linear regression to determine whether the relative influence of climatic vs edaphic factors was significantly correlated with study extent or grain. Furthermore, we extracted the 'threshold' extent and grain at which the relative effect of climatic and edaphic variables was equal (i.e. $y = 0$).

Results

Simulations

Analysis of simulated data sets revealed that, regardless of the ordination method or number of ordination axes used in its calculation, MESS was highly correlated with effect size statistics commonly reported in the literature (mean $r^2 = 0.78$–0.97; Table 2). We concluded that MESS is a valid measure of the effect of environmental predictor variables on community composition and included it in our analysis when other effect size statistics were not available.

Structure of the vegetation–environment data set

The 89 analyses from 63 studies that met our criteria for the meta-analysis covered a wide range of geographical regions, biomes, plant types and spatial scales. Geographically, we found analyses from six continents, with North America (35), Asia (20) and Europe (17) best represented. Analyses covered all major terrestrial biomes, but there was a bias towards temperate (36) and tropical forests (22), while other biomes such as savanna (4), temperate grassland (5) and tundra (3) were underrepresented. Most analyses included all vascular plants (23) or a subset of vascular plants, e.g. herbs, trees or specific clades (51), but some analyses also included nonvascular plants (bryophytes and lichens; 15).

There was considerable variation among studies in the methods used to collect and analyse vegetation data. Most analyses identified plants to the species level (85), but a few used higher (e.g. subspecies) or lower (genus) taxonomic resolution. To quantify community composition, most analyses measured percentage cover (32), cover classes (11) or presence/absence (24), although a variety of other measures, such as abundance, density, basal area and importance value, were also used. CCA was the most common multivariate data analysis method (41 analyses), followed by Mantel tests (25), DCA (14) and NMDS (9). Within these techniques, there was also large variation in

Table 2. Results of simulations to test the validity of the multivariate effect size statistic (MESS). Values are mean coefficients of determination (r^2) for relationships between MESS and standard measures of effect size derived from CCA and DCA.

Ordination	2 axes	4 axes
CCA (inter-set)	0.81	0.82
CCA (intra-set)	0.89	0.93
DCA	0.78	0.97

specific procedures, such as data standardization, distance metrics used to calculate dissimilarity matrices and effect size calculation.

On average, analyses included 10.8 total predictor variables belonging to 2.88 categories (median = 3). Edaphic variables were by far the most common, appearing in 87 of 89 analyses, but variables from our other primary category of interest, climate, were included in only 26 analyses (Table 3). Edaphic and climate variables were included together in only 23 analyses. Analyses including edaphics often measured a large number of edaphic variables (mean = 6.6), whereas analyses including climate tended to measure fewer climatic variables (mean = 3.0).

Among studies, extent varied by 10.5 orders of magnitude ($10^{-4.5}$–10^7 km^2), with a median of 158 km^2, and variable categories differed significantly in the extent of analyses in which they appeared (ANOVA, $F = 2.63$, $P = 0.02$). In particular, edaphic variables tended to be measured in studies with small extent (median = 132 km^2), whereas climatic variables tended to be measured in studies with large extent (median = 3425 km^2). There was a notable lack of studies ($n = 3$) that tested climatic variables at small extents (<10 km^2). Grain varied by 14 orders of magnitude ($10^{-3.3}$–$10^{8.8}$ m^2) among studies with a median of 200 m^2. There was no significant difference among variable categories in the grain of analyses in which they appeared (ANOVA, $F = 1.3$, $P = 0.27$).

Table 3. Primacy of predictor variable categories for extent and grain bin classes. Primacy values represent the percentage of cases where a given predictor variable category explained the most variance in species composition relative to the total number of analyses that analysed a variable of that category. The total number of cases is shown in parentheses.

Category	Extent (km^2)				Total*
	<1	1–100*	100–10 000	>10 000*	
Biotic	– (0)	0% (8)	0% (5)	50% (4)	12% (17)
Climatic	0% (4)	33% (3)	25% (8)	36% (11)	27% (26)
Disturbance	50% (4)	50% (10)	33% (9)	20% (10)	36% (33)
Edaphic	45% (20)	57% (21)	45% (29)	53% (17)	49% (87)
Spatial	0% (4)	0% (3)	29% (14)	0% (4)	16% (25)
Topographic	50% (18)	27% (15)	53% (19)	8% (13)	37% (65)

Category	Grain (m^2)				Total*
	<50*	50–200*	200–1000	>1000	
Biotic	0% (5)	0% (2)	67% (3)	0% (7)	12% (17)
Climatic	0% (5)	14% (7)	57% (7)	29% (7)	27% (26)
Disturbance	33% (9)	0% (2)	36% (14)	50% (8)	36% (33)
Edaphic	60% (20)	58% (26)	40% (25)	38% (16)	49% (87)
Spatial	25% (4)	0% (7)	17% (6)	25% (8)	16% (25)
Topographic	29% (14)	48% (21)	25% (16)	43% (14)	37% (65)

*Significant difference in primacy among predictor variable categories (chi-square test, α = 0.05).

Primacy

Across the entire data set, primacy differed significantly among categories of predictor variables (chi-square test, $P = 0.006$). Edaphic variables had the highest overall primacy (49%), meaning they were most likely to explain the most variation in plant community composition when tested, while biotic variables had the lowest primacy (12%; Table 3). There were few clear trends in the primacy of variable categories across extent classes. Primacy of disturbance variables decreased with increasing extent, but the sample size was fairly small (Table 3). Edaphic variables had the highest primacy in small-grained studies (<200 m^2), but their primacy tended to decrease with increasing grain (Table 3). No category was clearly superior in intermediate- (200–1000 m^2) or large-grained studies (>1000 m^2).
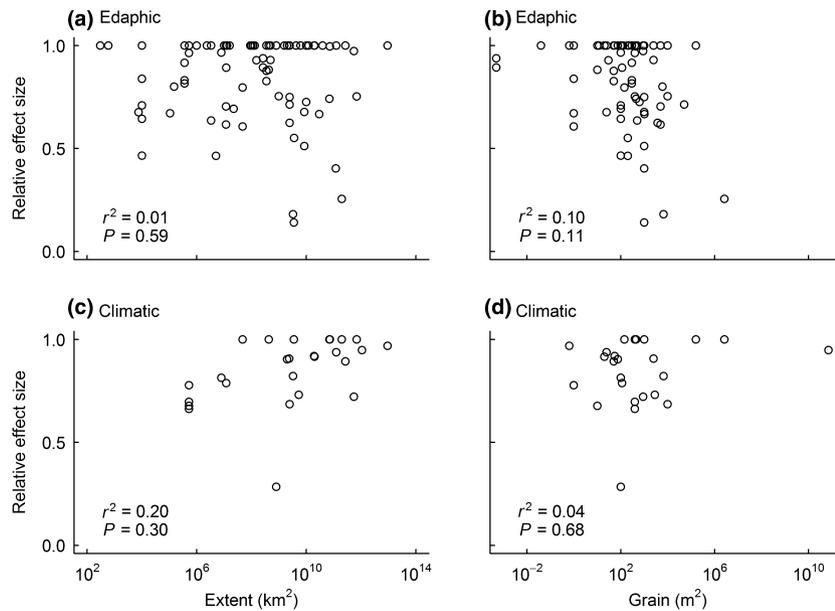
Relative effect size

Relationships between relative effect sizes of predictor variable categories and extent or grain were not statistically significant at the α = 0.05 level, but we detected trends that matched our initial hypotheses. The strongest trends were a decrease in the relative effect size of edaphic variables with increasing grain ($r^2 = 0.10$, $P = 0.11$; Fig. 2b) and an increase in the relative effect size of climatic variables with increasing extent ($r^2 = 0.20$, $P = 0.30$; Fig. 2c). Null model analyses showed that trends this strong could not have been produced by random variation of effect sizes within studies alone ($P < 0.001$). Relative effect sizes of the other predictor variable categories were not significantly correlated with extent or grain ($P > 0.3$).

Results from the analysis on the subset of studies that considered both edaphic and climatic variables suggest that the relative influence of edaphic vs climatic variables depends on extent and grain. As extent increased, the effect size of climatic variables increased relative to that of edaphic variables, although the relationship was only marginally significant ($r^2 = 0.20$, $P = 0.02$; Fig. 3a). The threshold value (i.e. the extent at which climatic variables superseded the importance of edaphic variables) was 1995 km^2 (or roughly a square region of 45 km per side; Fig. 3a). Climatic variables also became increasingly influential relative to edaphic variables at larger grains ($r^2 = 0.12$, $P = 0.09$; Fig. 3b). The threshold grain was estimated at 295 m^2 (Fig. 3b).

Discussion

We conducted a global meta-analysis to test for scale dependence in vegetation–environment relationships and

Fig. 2. Relative effect size of edaphic (**a** and **b**) and climatic variables (**b** and **c**) on community composition in relation to spatial extent and grain. Each point represents the variable with the largest effect size within a category in a given study. *P*-values, coefficients of determination and lines of best fit are from logistic regression of relative effect size on log-transformed extent or grain.

found trends broadly consistent with our initial hypotheses. The relative importance of different environmental factors as determinants of plant community composition was dependent on spatial scale. In particular, the influence of climatic variables increased relative to that of edaphic variables with increasing extent and grain (Figs 2 and 3). These results demonstrate the inherent scale dependence of ecological patterns (Levin 1992) and provide empirical support for one of the oldest observations in plant ecology. Schimper (1903) was among the first plant geographers, and influenced by the work of Warming (1895), estab-

lished a set of 'rules' (Kruckeberg 2004) that included (1) climate as the primary determinant of plant composition worldwide (i.e. at broad scales) and (2) soil properties of secondary importance, predominantly within regions (i.e. at fine scales). Although it took many decades for plant ecologists to develop the appropriate statistical tools and data sets required to refine Schimper's assertion, we find it nonetheless surprising that such investigations have been lacking despite the large growth of quantitative vegetation–environment studies since the 1980s (von Wehrden et al. 2009).
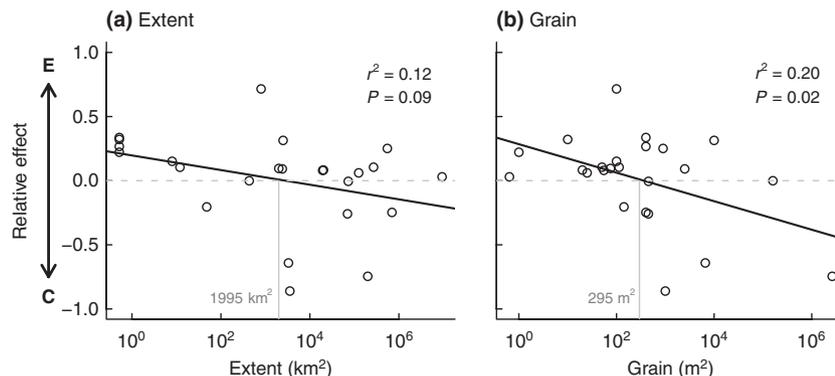
Fig. 3. Comparison of the relative effect of edaphic vs climatic factors on community composition as a function of spatial extent (**a**) and grain (**b**). The analysis only considered the subset of studies that included climatic and edaphic factors simultaneously (*n* = 23). Each point represents the difference between the relative effect size of the most explanatory edaphic and climatic variable in a given study. Values greater than zero (dashed grey line) indicate that edaphic variables are better predictors of community composition than climatic variables, and vice versa. Black lines represent linear models. Solid grey lines represent scale thresholds at which the transition from a primary edaphic influence to a primary climatic influence occurs.

The transition from edaphic to climatic factors as the primary drivers of spatial turnover in composition as scale increases, and spatial extent in particular, suggests there is a threshold extent, which we estimated is approximately 2000 km^2, where climate and soils are roughly equal drivers of vegetation–environment correlations (Fig. 3). If accurate, we suggest this area is an emergent scale threshold defining the primary cause of different structures of spatial variation in atmospheric (coarse-grained) vs edaphic (fine-grained) factors, and, secondarily, how those factors interact to limit plant distribution. For example, 2000 km^2 – or a linear distance of about 45 km – should be roughly the distance threshold at which plant species from different plots are more likely to differ in temperature tolerances than pH tolerances, based simply on how variance in those factors is spatially distributed (Fig. 1a). Of course, the 2000 km^2 threshold should not be considered a hard rule, and the actual scale of transition will likely vary depending on other factors, particularly topographic relief, which strongly influences the spatial distribution of climatic variation (Palmer 2007). If plant ecologists had a better understanding of such environmental distributions, for example by applying geostatistical tools to describe spatial structure in environmental data (Rossi et al. 1992; Urban et al. 2000), we would be better able to design surveys with strong statistical power to detect basic plant–environment associations.

Although the concept of spatial extent and its potential to influence vegetation–environment relationships is perhaps more intuitive, we find it interesting that grain was at least as important in determining the relative influence of different environmental factors on plant communities (Figs 2 and 3). It is probably not surprising that edaphic variation would strongly influence plant community composition within, for example, a 1-ha area of forest, and that increasing the study extent to continental scale would result in an increase in the relative influence of climate. We suspect that few plant ecologists appreciate that a similar shift in the relative importance of edaphic and climatic factors could result from increasing the size of sampling plots (i.e. grain), without any change in the extent of the study. Our analysis identified a threshold grain of approximately 300 m^2 at which climatic factors became better predictors of community composition than edaphic factors. We argue that this transition occurs because, at large grain sizes, most fine-scale edaphic variation is included within plots, leaving little between-plot variation to explain variation in community composition. Supporting this interpretation, edaphic variables were more sensitive than climatic variables to increasing grain (Fig. 2b,d). These results stress the importance of carefully considering the size of plots used in vegetation studies in relation to the scale of spatial variation of the environmental variables being considered,

as this decision can have a strong influence on the observed vegetation–environment relationships (Fortin et al. 1989; Reed et al. 1993; Fortin & Dale 2005).

Our findings regarding the spatial dependence of vegetation–environmental relationships complement the insights gained through studies of spatial patterns of biodiversity, such as species–area relationships. Interestingly, our estimated spatial extent threshold, 2000 km^2, coincides with the scale at which triphasic species–area curves often shift from phase 2 (shallow) to phase 3 (steep) (Fridley et al. 2005, 2006; Fridley, unpublished data), in line with Palmer's (2007) environmental texture hypothesis. This hypothesis asserts that species diversity in a given area is driven by the amount and distribution of environmental heterogeneity (i.e. environmental 'texture'), which itself varies as a function of spatial scale. Drawing links to this hypothesis, we suggest that at fine spatial scales, spatial variation in edaphic variables drives spatial turnover of plant community composition, generating strong vegetation–edaphic relationships and an accumulation of new species with increasing area (i.e. steep species–area curve). At intermediate scales, edaphic variation plateaus, leading to a relatively weaker influence of soils on vegetation and a shallow species–area curve. At broad scales (>2000 km^2), climatic variation becomes large enough to drive spatial variation in community composition, leading to strong vegetation–climate relationships and a steep species–area curve. Future studies that combine information on spatial patterns of species diversity, spatial turnover in community composition and spatial variation of environmental variables should refine our understanding of how plant communities are structured in space.

We were primarily interested in edaphic and climatic factors, but we also tested for spatial dependence of the influence of a variety of other environmental variables (biotic, disturbance-related, spatial and topographic). These factors often explained a large amount of variation in community composition (Table 2), but there were no consistent trends in their relative effect in relation to spatial extent or grain. The reason for a lack of clear relationships may be that, unlike edaphic and climatic variables, variables within these categories do not have a characteristic scale of spatial variation. For example, while we argue that variation in edaphic variables is characteristically fine-grained and variation in climatic variables is coarse-grained, the 'disturbance' category included variables as diverse as grazing intensity, human land use and glaciation, which represent processes that occur on vastly different spatial scales. Analysing patterns of more narrowly defined categories of environmental variables would probably have been more informative, but the small sample size of our analysis did not allow this.

The largest challenge to detecting general patterns in this study was the inconsistency among studies in the methods used to analyse and report vegetation–environment relationships. A diverse variety of statistical methods exist for analysing multivariate community data (von Wehrden et al. 2009), and direct comparisons of results even among studies using similar methods are potentially misleading. We will not debate the relative merits of different ordination and other multivariate analysis methods here, as that topic has received considerable attention elsewhere (e.g. Kent & Ballard 1988; Palmer 1993), but we do recommend that, regardless of the method used, studies should report a single effect size statistic for each environmental variable that quantifies the amount of variation in community composition explained by that variable, rather than (or in addition to) reporting correlations with individual ordination axes. Specifically, we recommend that studies report the following effect size statistics: (1) CCA – proportion of total inertia in CCA explained by environmental variable (ratio of eigenvalue to total inertia; Økland & Eilertsen 1994); (2) DCA and NMDS – coefficient of determination (r^2) of linear or surface model of environmental variable fit to the ordination (Dargie 1984); (3) Mantel test – Mantel's r. This will allow simpler interpretation of the relative influence of different environmental factors measured in a study on community composition, and facilitate comparisons among studies that can lead to a more general understanding of vegetation–environment relationships.

In summary, our meta-analysis provided evidence that the relative influence of different environmental variables on plant community composition depends on spatial scale, with the effect of climate increasing relative to that of edaphic factors with increasing extent and grain. These results supported our initial hypotheses based on differences in the spatial distributions of edaphic (fine-grained) and climatic (coarse-grained) variables, suggesting that an awareness of the spatial structure of the environment is critical for measuring and understanding vegetation–environment relationships. Our analysis was complicated by the difficulty of summarizing results of vegetation studies using diverse methods. Given the recent availability of large vegetation data sets from large regions across the world, our hypotheses could be further tested by conducting a similar analysis using a standard methodology on a single data set, varying both spatial extent and grain.

Acknowledgements

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Supporting Information

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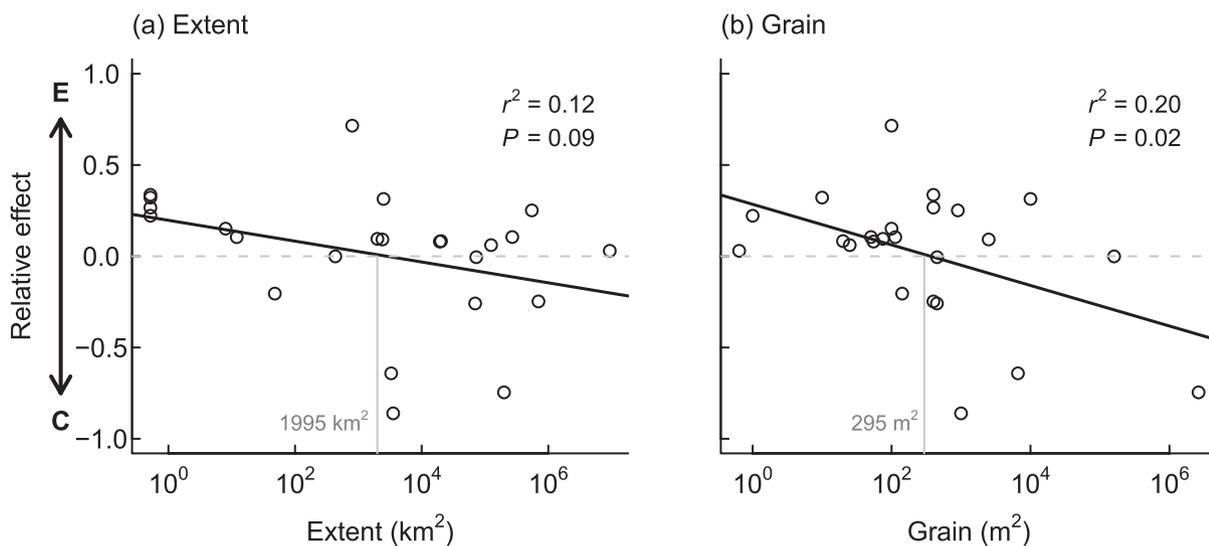
Appendix S1. Summary of vegetation studies used in the meta-analysis.
Appendix S2. Description of simulation to test the multivariate effect size statistic (MESS).

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Graphical Abstract

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(a) Extent — $r^2 = 0.12$, $P = 0.09$, threshold 1995 km², axes Relative effect (E to C) vs Extent (km²).
(b) Grain — $r^2 = 0.20$, $P = 0.02$, threshold 295 m², axes Relative effect vs Grain (m²).

We conducted a global meta-analysis of vegetation studies and found that the relative importance of different environmental factors as determinants of plant community composition varied with spatial scale. In particular, the importance of climate factors relative to edaphic factors increased with increasing spatial extent and grain, with scale thresholds of about 2000 km² for extent and 300 m² for grain.