

# The distance decay of similarity in ecological communities

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Biological similarity typically decreases with geographical distance. Despite the recent attention to the distance decay relationship, there is no consensus on how the relationship varies across organism groups, geographic gradients and environments. We first conducted a quantitative meta-analysis of 401 distance decay relationships across a wide range of organisms, ecosystems and geographical gradients, and then united the effects of categorical and continuous variables on the rate of distance decay using a general linear model (GLM). As effect sizes we used the similarity at one km distance (initial similarity) and the distance that halves the similarity from its value at one km distance (halving distance). Both the initial similarity and halving distance were significantly affected by variables characterizing the spatial scale, organism properties, study region and ecosystem concerned. The patterns appear robust as the results of meta-analysis and GLM only differed in marginal details. According to GLM with Akaike's information criterion, the most parsimonious models explained 55.3 and 37.6% of variance in initial similarity and halving distance, respectively. Across large scales, similarity was decreasing slightly faster at high latitudes than at low latitudes, while small-scale turnover was higher at low latitudes. We also found significant differences in initial similarity among the realms, with terrestrial systems showing higher small-scale beta diversity. The decrease in community similarity at large scales was higher among organisms that are actively mobile than among passively dispersed organisms. We conclude that regression of similarity against distance unites several ecological phenomena such as dispersal propensity and environmental structuring, and provides an effective approach for gauging the spatial turnover across sites. We also found that the patterns in beta-diversity are highly scale-dependent.

The decay of community similarity with geographical distance has been recognized by ecologists for several decades. The decrease in similarity of any two observations with distance was first underlined by geographers (Tobler 1970), and many ecological phenomena incorporate the pattern of decreasing community similarity with geographical distance (Nekola and White 1999). The distance decay of similarity in ecological communities can be accounted for by at least three mechanisms. First, similarity decays with distance because of decreasing similarity in environmental features. Following Nekola and White (1999), this could be attributed to niche-based community processes, with species differing in their ability to perform under different environmental conditions (Tuomisto et al. 2003, Gilbert and Lechowicz 2004). In meta-community ecology, this process has been referred to

species-sorting (Leibold et al. 2004). Second, spatial configuration and the nature of the landscape dictate the dispersal rate of organisms among sites. In a landscape with major dispersal barriers, community similarity decreases more abruptly than in open and topographically homogeneous settings (Garcillán and Ezcurra 2003). Third, according to neutral theory (Hubbell 2001), community similarity decays with distance even if the environment is completely homogeneous, due to organisms' limited dispersal. Typically, the smoothest distance decay relationships are produced by neutral theory, as similarity is not affected by environmental heterogeneity, but rather by ecological drift, random dispersal and random speciation (Hubbell 2001). We emphasize that these three main processes are not mutually exclusive, and the rate of distance decay is in most communities probably jointly

controlled by niche-based processes, spatial configuration and neutrality (Tuomisto et al. 2003, Cottenie 2005).

Despite the recent interest in distance decay relationship, there is no consensus on how the relationship varies across organisms and environments. Most of the studies to date have been conducted in terrestrial ecosystems and have examined the distribution patterns of vascular plants either in tropics or in boreal region (Nekola and White 1999, Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Qian et al. 2005). Studies have shown that the relationship between plant community similarity and distance can be typically approximated by a logarithmic model suggesting non-random propagule rain, and have generally lent only a weak support for neutrality (Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Dornelas et al. 2006). A number of studies have also examined the distance decay of marine fish parasite communities (Poulin 2003, Oliva and González 2005), or distance decay among insects and mammals (Harrison et al. 1992, Wiersma and Urban 2005, Lloyd et al. 2005, McDonald et al. 2005, Thompson and Townsend 2006). Recently, there has also been a growing interest in examination of distance decay of microbial communities (Green et al. 2004). The synthesis of factors affecting the distance decay is, however, still lacking. For the related issue of meta-communities, Cottenie (2005) analysed a number of assemblages together with their environmental and spatial correlates to see whether these confirm more to neutral model or species-sorting theory. The results suggested that species-sorting was by far the strongest structuring force for the major part of the communities, although much of the community variation was also attributed to spatial factors.

According to recent meta-analyses on the latitudinal diversity gradient (Hillebrand 2004), species-area relationships (Drakare et al. 2006), and hierarchical beta diversity (ratio of regional to local species richness; Soininen et al. unpubl.), the distance decay relationship should exhibit predictable variation across organism groups, geographical gradients and environments. For example, the rate of decline in similarity would be greater for organisms with lower dispersal ability resulting in faster decay of similarity with distance. This is because among highly vagile organisms, across-site dispersal results in larger homogenization of communities, and spatial variation in community structure is thus mainly attributable to variation in species fitness under varying environmental constraints (Finlay et al. 1996, Horner-Devine et al. 2004, Thompson and Townsend 2006). High dispersal rate will also compensate for low population persistence through mass- or rescue-effects (Brown and Kodric-Brown 1977, Shmida and Wilson 1985). On the other

hand, small organisms, which respond more intensively to fine scale variation in the environment due to their shorter generation times (Gillooly et al. 2002), will have lower similarity at small distances (Fig. 1). In addition to the properties of the environment and the organism, the rate of similarity decay with distance might also vary across latitude as there is a general latitudinal gradient in hierarchical beta diversity (Soininen et al. unpubl., but see Willig and Gannon 1997, McKnight et al. pers. comm.). Finally, distance decay varies with both the spatial extent and grain size of the study (Nekola and White 1999). Generally, the rate of decay in similarity should be larger for smaller study extents, and larger grain size should result in higher similarity among the sites. However, these general patterns may be altered if the study area crosses evolutionary provinces, where the assemblages do not have a shared evolutionary history.

Here, we conducted a quantitative meta-analysis of distance decay relationship across organisms and environments. We used as effect sizes both the similarity at one km distance and the halving distance, which is

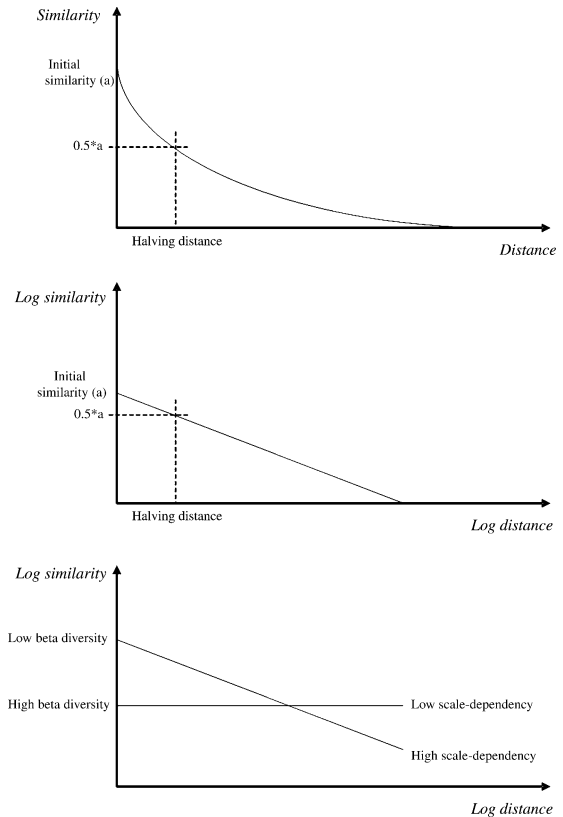


Fig. 1. Conceptual figure denoting the initial similarity and halving distance (i.e. the distance that halves the similarity from its maximum) of distance decay relationship in linear space (upper figure) and logarithmic transformed space (figure in the middle). The lower figure describes low and high beta diversity, and low and high scale-dependency of beta diversity.

the distance that halves the similarity from its value at one km distance (Fig. 1). For simplicity, we refer to the former as “initial similarity” throughout the paper. The initial similarity reflects beta diversity (i.e. turnover in species composition from site to site) at small spatial extents, and high initial similarities mirror low beta diversity. The halving distance reflects the rate of species turnover per unit distance, being thus a measure of the scale-dependency of beta diversity. Large halving distances indicate that the rate of species turnover change little with increasing spatial scale, while short halving distances imply that species turnover is highly scale-dependent. The major advantage of the halving distance over any measure of slope is that it can be calculated for any type of regression between similarity and distance, and offers thus a highly useful and easily comprehensible metric for among-study comparisons. We tested the following predictions: 1) initial similarity (i.e. the similarity at one km distance): we predict that the initial similarity will increase with body size, as smaller organisms are especially sensitive to fine scale variation in environment. Since hierarchical beta diversity is high at low latitudes reflecting beta diversity at relatively small scales (Soininen et al. unpubl.), the initial similarity should be lower in low latitudes than in high latitudes. 2) Halving distance: we predict that the halving distance is shorter for larger organisms due to lower dispersal ability (Finlay et al. 1996, but see Martiny et al. 2006). Moreover, we predict that the halving distance is shorter for organisms that disperse via passive means. Since beta diversity is higher in low latitudes than in high latitudes (Soininen et al. unpubl.), we also predict that the halving distance becomes shorter towards the equator. Since organisms at high trophic position have steep gradients in alpha diversity (Hillebrand 2004), we predict that the halving distance is shorter for organism at high trophic position. Finally, we predict that the halving distance is shorter for smaller study extents.

## Material and methods

The data were drawn from studies that report the relationship between community similarity and geographical distance (i.e. slope and intercept of the relationship). Two abstracting services were searched: ISI Web of Knowledge (1980–2005) and Aquatic Sciences and Fisheries Abstracts (1980–2005). The search strings were “similarity and distance”, “dissimilarity and distance” and “distance and decay”. More recent papers were included if present, and also papers derived from bibliographies of the papers that were screened. We also included some unpublished results to the analysis. In total, we assembled 401 distance decay relationships. For a detailed list of studies included, see Appendix 1.

Each distance decay relationship was described using both the initial similarity and halving distance (see definitions below). We included studies where similarity was presented using Jaccard (J) or Sorensen (S) similarity measures that range from 0 to 1. Moreover, we included relationships published by Harrison et al. (1992), where similarity is presented using a modified Whittaker beta diversity measure:  $[(S/a) - 1]/(N - 1)$ , where S is regional diversity, a is mean alpha diversity and N is the number of sites. For a reliable comparison of similarities across the studies, we transformed all the initial similarities (see definition below) to Sorensen metrics, using the identity  $S = 2J/(1 + J)$ .

We calculated all halving distances analytically by using the published regression coefficients. We used three different calculations depending on the form of the original regression: linear-linear, log-linear, or log-log. In the last form, where log similarity is related to log distance, there is no true intercept as  $y = \infty$  when  $x = 0$ . Therefore, we defined two metrics that could be calculated for all three regression forms, and were ecologically meaningful. First, we calculated the similarity at one km distance – initial similarity, as this scale was most applicable for most of the data used. For the linear-linear regression form,  $\text{Sim}(1) = \beta \times 1 + \alpha$ , where  $\beta$  and  $\alpha$  are the published regression parameters. For the log-linear regression form,  $\text{Sim}(1) = \exp(\beta \times 1 + \alpha)$ . For the log-log regression form,  $\text{Sim}(1) = \exp(\alpha) \times 1^\beta$ . Second, we calculated how much further apart sites would have to be to halve the similarity at one km distance – the “halving distance”. For the linear-linear regression form, the halving distance is  $(\beta - \alpha)/2\beta$ . For the log-linear regression form, the halving distance is  $1 - \log 2/\beta$ . For the log-log regression form, the halving distance is  $2^{(-1/\beta)}$ . Where necessary, the halving distance was transformed to kilometres from meters.

Each distance decay relationship was classified with respect to three continuous variables (organism body weight, latitude of the center of a study area and spatial extent of the study), and five categorical variables (organism dispersal type, realm, study region, thermo-regulation and trophic position). Most of the studies included did not show detailed information on the grain of the study, and therefore we were unable to address the effect of grain size on distance decay. Latitude was scored from 0 to 90, no matter whether the study region was located in northern or southern hemisphere. Organism body size was approximated as log transformed wet weight (g), and derived for each organism group from published sources (Peters 1983, Hillebrand 2004). For more details on body size approximations and ecological classifications, see Hillebrand (2004) and Drakare et al. (2006).

We used unweighted fixed model meta-analysis (Gurevitch and Hedges 1993) to test the effect of the variables described above. The number of sampling sites

was not correlated with the slope or the intercept of the distance decay regression (e.g. for the slope,  $r^2 = 0.02$ ,  $p = \text{n.s.}$ ). Therefore, we did not need to weight the analysis. For overall and group-wise average effect sizes, 95% confidence intervals were calculated using a bootstrapping procedure with 999 permutations (Rosenberg et al. 2000). The null hypothesis was that there are no differences in test statistic among the groups. The meta-analyses were conducted using the software package MetaWin 2.0 (Rosenberg et al. 2000).

We used general linear model (GLM) with best model selection to unite the effects of categorical and continuous variables on distance decay. We included four categorical variables (dispersal type, thermoregulation, trophic position and realm), three continuous variables (latitude, log body weight and log extent), as well as the interactions between dispersal type and body weight and thermoregulation and body weight, respectively. The continuous variables did not show strong inter-correlations ( $r^2 < 0.025$  for all relationships), and therefore we included these variables in the models without a need to remove the multicollinearity. For the interpretation of our results, it was especially important that study extent and latitude were not correlated. We identified the most parsimonious models using Akaike's information criterion (Burnham and Anderson 1998). The general linear model was conducted using software package Statistica 6.0.

## Results

### Initial similarity

The grand mean effect size for the initial similarity across all studies was 0.875 (95% CI: 0.857–0.892). The total heterogeneity implied significant structure in the effect sizes ( $Q_{\text{tot}} = 14.1$ ,  $p = 0.001$ ).

As we predicted, the initial similarity exhibited a positive, albeit non-significant, relationship to latitude, i.e. the initial similarity was slightly higher at high latitudes (Fig. 2a, Table 1). The initial similarity also varied significantly among the realms, and terrestrial systems showed notably high values (Fig. 2b). The initial similarity exhibited significant variability among the study regions, as the studies conducted in the New World had the highest initial similarities (Fig. 2c). The initial similarity also highlighted the importance of study extent on distance decay, since there was a strong negative relationship between the initial similarity and log study extent (Fig. 2d).

The results of the meta-analysis showed that the initial similarity is not only controlled by environment or geographical gradients, but also correlates with organism characteristics. The initial similarity varied significantly among the organisms with different dis-

persal type, and it was highest in organisms that move on the ground, fly or disperse via pelagic larvae (Fig. 2e). Organisms dispersing via spores had notably low initial similarities. Largely paralleling the results regarding dispersal type, we found that homiotherms (i.e. birds and mammals) had significantly higher initial similarities than the ectotherms (Fig. 2f). Likewise, there were significant differences in initial similarity among the organisms with different trophic position (Fig. 2g). Autotrophs, herbivores and carnivores showed all nearly comparable initial similarities, and these were highest among omnivores. Finally, initial similarity showed a significant positive relationship with organism body weight (Fig. 2h).

### Halving distance

The grand mean effect size for log halving distance across all studies was 2.806 (95% CI: 2.756–2.851), or a reduction in the initial similarity of 50% in 639 km. The total heterogeneity implied significant structure in the effect sizes ( $Q_{\text{tot}} = 90.3$ ,  $p = 0.001$ ).

Contrary to what was initially predicted, there was a significant negative relationship between log halving distance and latitude, as the decay of similarity with distance was faster in studies conducted in higher latitudes (Fig. 3a, Table 1). We did not find significant differences in halving distance among the realms, although the halving distances were longest in marine systems (Fig. 3b). The rate of distance decay showed large-scale longitudinal patterns, as halving distance differed significantly among the study regions. Studies conducted in the Pacific had the longest halving distance, and the similarity was decreasing most rapidly in Eurafica (Fig. 3c). The halving distance also exhibited a significant positive relationship with the study extent, as we predicted (Fig. 3d).

Besides reflecting the characteristics of the environment or geographical position of the study, halving distances varied widely among the organism groups and among organisms' major characteristics. First, we found significant differences in halving distances among the organism dispersal type. In contrast to what was predicted, halving distances were not shorter for organisms that disperse via passive means, but rather were similar to other organisms (Fig. 3e). The halving distances varied also significantly between the ectotherms and homiotherms as the latter had slightly longer halving distances (Fig. 3f). As we predicted, the halving distances became generally slightly shorter with the increasing trophic position in a food web (Fig. 3g). This trend was not clear-cut, however, since groups such as autotrophs also had relatively short halving distances. The rate of decay in community similarity was clearly highest among carnivores. Finally, the

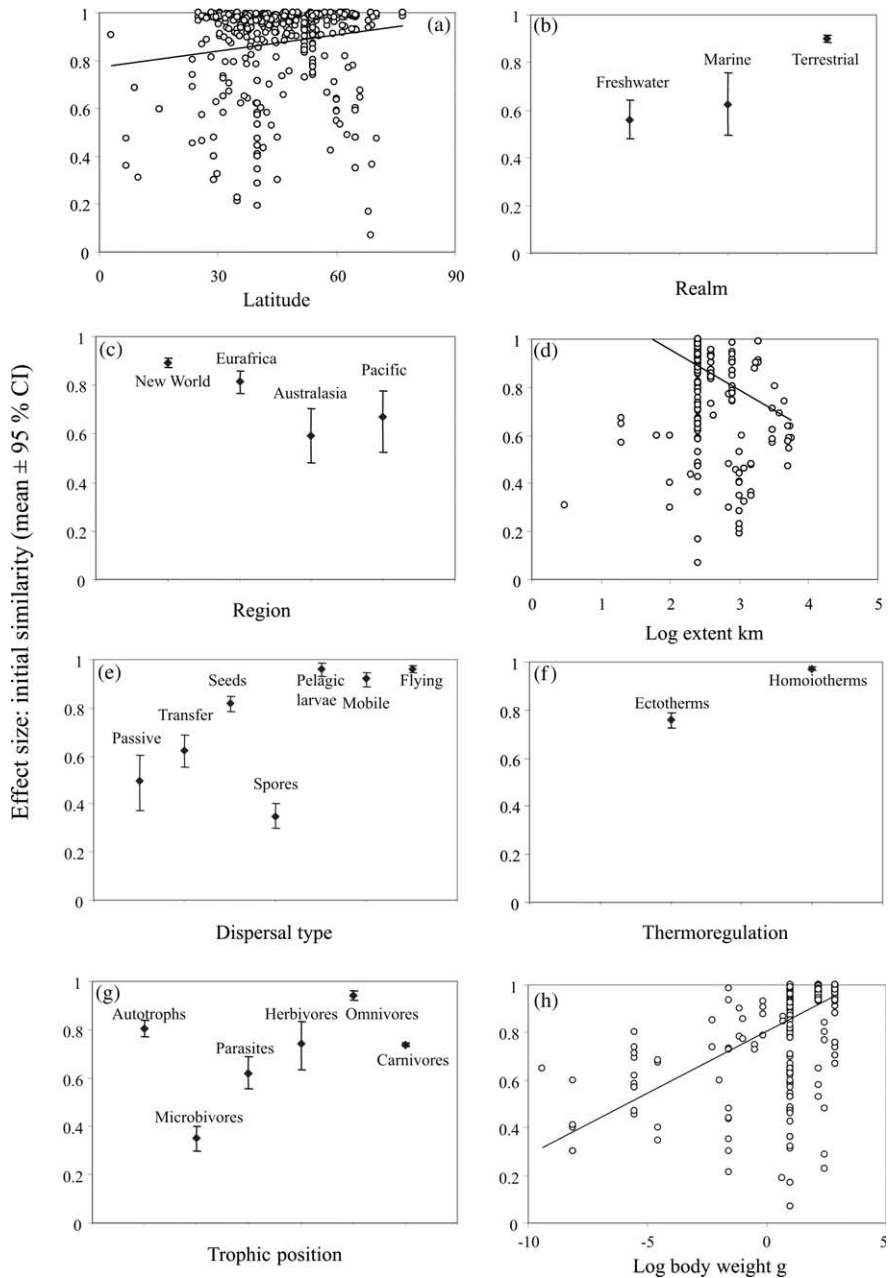


Fig. 2. Mean effects ( $\pm 95\%$  confidence intervals) of a) latitude, b) realm, c) region, d) study extent, e) organism dispersal type, f) thermoregulation, g) trophic position and h) body weight on initial similarity (i.e. similarity at one km distance).

halving distances did not show significant relationship with the organism body weight (Fig. 3h).

## Synthesis

According to GLM with Akaike's information criterion, the most parsimonious models for explaining the variance in the initial similarity and halving distance

incorporated several variables and therefore implied that the distance decay was simultaneously correlated with a variety of factors (Table 2). The most parsimonious GLM model for the initial similarity explained 55.3% of variance in the data (Table 2), and incorporated most of the variables initially entered. The impact of these factors on the initial similarity was generally similar to that of the meta-analysis since study extent and latitude had similar kind of relationships. However, when

Table 1. Results of fixed-model meta-analysis of initial similarity (i.e. similarity at one km distance) and halving distance in respect to different factors. P values refer to significances obtained by bootstrapping procedure with 999 permutations and B refers to slope of the regression model.

Variable	Initial similarity (k =401)		Halving distance (k =401)	
	p	B	p	B
Latitude	n.s.	0.002	<0.05	-0.004
Realm	0.001		n.s.	
Region	0.001		0.001	
Log extent	0.001	-0.168	<0.01	0.423
Dispersal type	0.001		0.001	
Log body weight	<0.05	0.052	n.s.	-0.011
Thermoregulation	0.001		0.001	
Trophic position	0.001		0.001	

controlling for the effects of latitude and study extent, marine systems showed the highest initial similarities thus differing from the results of the meta-analysis.

For the halving distance, the most parsimonious model explained 37.6% of variance, and included most of the factors initially entered. The results resembled those obtained for the meta-analysis, as in both analyses the study extent showed a positive relationship with the halving distance (Table 3). GLM results differed from those emerging from meta-analysis only in marginal details. When controlling for the effect of the study extent, microbivores had the longest halving distances thus disagreeing with the results of the meta-analysis.

## Discussion

The lower initial similarities at lower latitudes implied higher small-scale beta diversity near the tropics. This finding is congruent with the results of a recent meta-analysis of hierarchical beta diversity (i.e. ratio of regional to local species richness) (Soininen et al. unpubl.). However, we found a negative relationship between halving distance and latitude. This slightly faster decay of similarity at higher latitudes contradicts our expectations, and also disagrees with Rapoport's rule, which predicts a positive correlation between range size and latitude (Stevens 1989). Note that in earlier studies the latitudinal variation in turnover diversity has not been clear-cut, given that some researchers have not found any evidence on latitudinal gradient in turnover (Harrison et al. 1992, Willig and Gannon 1997, McKnight et al. pers. comm.). Bowman (1996) even reported a similar positive relationship between latitude and turnover in plants in Australia. The explanation for the pattern we found remains speculative at present but at least three factors can be put forward. First, the result could stem from higher large-scale variability in climate at high latitudes. This is because the major part of the community residents was typically interchanged among the sites at the scale of ca 1000 km, and the shifts in

community composition corresponded therefore more to large-scale variability in environmental features. Second, beta diversity shows different latitudinal gradients depending on the scale of the study. Some support for this hitherto unprecedented pattern comes from a recent meta-analysis of species-area relationship (Drakare et al. 2006). At small scales ( $< 1 \text{ km}^2$ ), slope of the species-area relationship is decreasing with latitude ( $R^2 = 0.135$ ,  $n = 293$ ,  $p = 0.000$ ; Fig. 4). By contrast, at large scales ( $> 1 \text{ km}^2$ ), slope of the species-area relationship is slightly, though non-significantly, increasing with latitude ( $R^2 = 0.001$ ,  $n = 215$ ,  $p = \text{n.s.}$ ). Third, the pattern we found may have also been influenced by the fact that the similarity indices are affected by variability in diversity, which increases under low species richness, i.e. towards higher latitudes (Lennon et al. 2001). Any between-site change among community residents in a species poor region results therefore in a larger change in community similarity than a corresponding change in a community in a more diverse region.

The relationship between the log extent and the halving distance was significant and positive. Given that the spatial extent was incorporated into the most parsimonious model with a positive effect in GLM, our data corroborated the prediction of longer halving distance with increasing study extent (Nekola and White 1999). The study extent played also a major role in determining the initial similarity, as the extent and the initial similarity exhibited a significant negative relationship. The large residual variation in the relationships between the study extent and both the halving distance and the initial similarity implies, however, that the distance decay is not only dictated by spatial scale, but is also affected by the organism properties and the strength of environmental gradients (Nekola and White 1999, Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Horner-Devine et al. 2004, Thompson and Townsend 2006). Stronger environmental gradients should generally result in shorter halving distances and lower initial similarities, yet these relationships

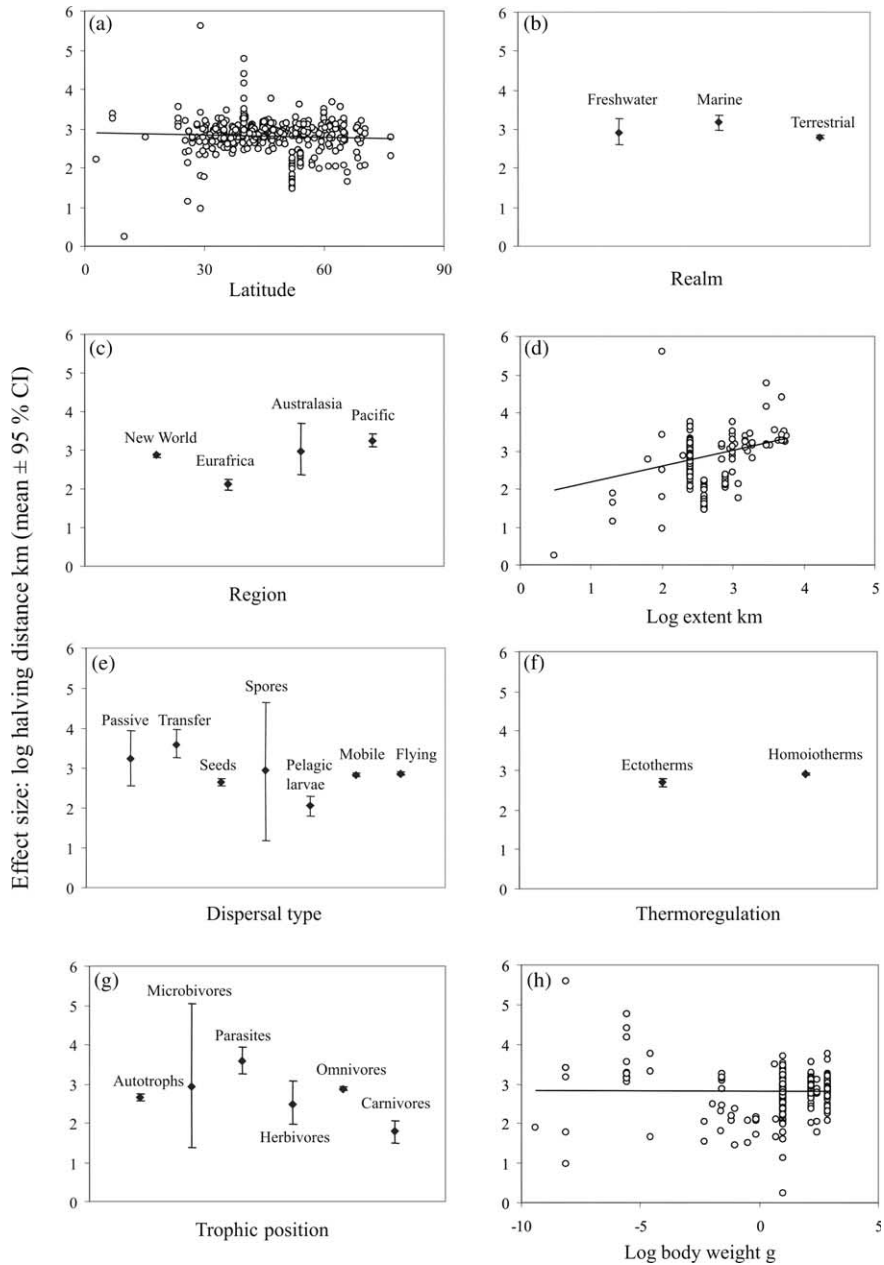


Fig. 3. Mean effects ( $\pm 95\%$  confidence intervals) of a) latitude, b) realm, c) region, d) study extent, e) organism dispersal type, f) thermoregulation, g) trophic position and h) body weight on log halving distance.

Table 2. The most parsimonious models for explaining the variance in initial similarity and halving distance of the distance decay relationship. The modelling was conducted using a general linear model with Akaike's information criterion for best model selection. For the factors that were used for explaining the variance in distance decay, see Material and methods. The interactions between the variables are marked with an asterisk.

Effect size	Model	N	F	R <sup>2</sup>	p
Initial similarity	Dispersal type+thermoregulation+trophic position+realm+log extent+latitude+dispersal type $\times$ log body weight	401	27.70	0.553	0.00
Halving distance	Dispersal type+trophic position+realm+log extent+dispersal type $\times$ log body weight+thermoregulation $\times$ log body weight	401	14.32	0.376	0.00

Table 3. Results of the GLM analyses for the distance decay relationships.

Effect size	Variable	SS	DF	MS	F	p	Constant	SE
Initial similarity								
	Dispersal type	0.2446	3	0.0815	5.0059	0.0020		
	Thermoregulation	0.0978	1	0.0978	6.0036	0.0147		
	Trophic position	0.2611	3	0.0870	5.3426	0.0013		
	Realm	0.0986	2	0.0493	3.0267	0.0496		
	Log extent	0.1024	1	0.1024	6.2884	0.0126	-0.0623	0.0248
	Latitude	0.0624	1	0.0624	3.8328	0.0501	0.0010	0.0005
	Dispersal type $\times$ log body weight	0.1452	4	0.0363	2.2295	0.0653		
	Error	6.1895	380	0.0163				
Halving distance								
	Dispersal type	3.6465	3	1.2155	8.3242	<0.0001		
	Trophic position	1.4144	3	0.4715	3.2288	0.0225		
	Realm	0.8901	2	0.4454	3.0508	0.0485		
	Log extent	8.8236	1	8.8236	60.4269	<0.0001	0.5771	0.0742
	Dispersal type $\times$ log body weight	4.0351	4	1.0088	6.9084	<0.0001		
	Thermoregulation $\times$ log body weight	1.6268	1	1.6267	11.1407	0.0009		
	Error	55.6339	381	0.1460				

also depend on environmental tolerances of the organisms present. Cottenie (2005) assembled the meta-community data from published sources to examine the relative proportions of environmental and spatial structuring in communities, and found that species sorting was the strongest mechanism in accounting for the variation in community composition, thus emphasizing the role of niches and environmental constraints in structuring communities. Yet, the analyzed communities were also strongly spatially structured suggesting some degree of dispersal limitation, and lending thus support not only to local niche-based processes, but also for neutrality.

Given the general importance of niche-based processes, the lack of data on environmental heterogeneity presents a possible caveat for our approach in general.

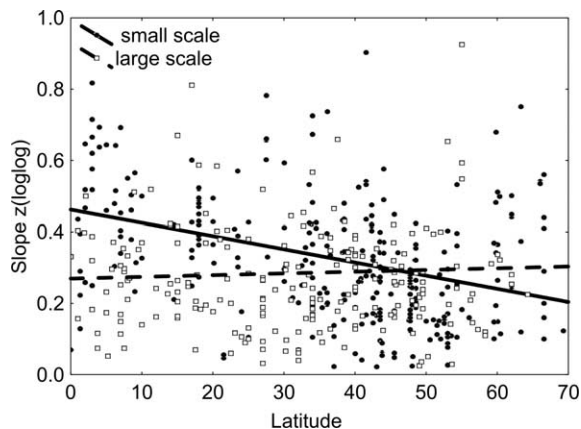


Fig. 4. The relationship between latitude and the slope of the species-area relationship for the small scales ( $<1 \text{ km}^2$ ) and the large scales ( $>1 \text{ km}^2$ ). For the details of the data used, see Drakare et al. (2006). Due to clarity, five data points are missing from the figure, but they are included in regressions.

However, as spatial extent in many of our data sets was exceedingly large, ranging up to six thousand kilometers, among-organism variability in dispersal capacity may have had a large effect on our results. Moreover, although we lack detailed information on environmental heterogeneity, we could make general suggestions of the degree to which environmental variability account for community variation in each of the three realms resting upon their known heterogeneity in general. We found significant differences among the realms only for the initial similarity, although generally more homogeneous marine systems exhibited slightly longer halving distances than more heterogeneous freshwater or terrestrial systems, thus perhaps suggesting slightly lower turnover in oceans. Although the pattern is intuitively reasonable, it slightly contradicts to recent meta-analyses on latitudinal diversity gradient (Hillebrand 2004) and beta diversity (Soinin et al. unpubl.), which showed that despite their homogeneity, marine systems do show strong gradients in diversity that are comparable to those found for freshwater or terrestrial systems. However, given that the initial similarities were clearly lower in marine systems than in terrestrial realm, these data also imply that the small-scale turnover may be relatively high in oceans. Moreover, the study extent in marine systems was generally very large, thus increasing the halving distances. Besides showing faster decay of similarity at large scales (shorter halving distances), terrestrial systems showed notably high initial similarities, thus showing lower turnover at small spatial extents. This further highlights the scale-dependency in beta-diversity (Martiny et al. 2006). We also found that the initial similarities were lowest in freshwaters. The high small-scale beta diversity in freshwaters is reasonable given that they are typically highly fragmented in terrestrial matrix even at small spatial extents.



We did not find any evidence that organisms with passive dispersal would show shorter halving distances than organisms with active mobility. Rather, we found that the rate of decrease in community similarity was higher among organisms that are move on the ground or fly (Thompson and Townsend 2006). The independent effect of dispersal type on the pattern we found was evidenced by the fact that dispersal type was incorporated in GLM for the halving distance. This pattern was partly explained by differences in body size as there was a slight, though non-significant, negative relationship between body size and halving distance. Homiothermic, mobile birds and mammals showed generally slightly shorter halving distances than smaller passive organisms, but their initial similarities were higher. This corroborates our prediction of increasing initial similarities with increasing body size, and reflects perhaps the higher small-scale beta diversity for smaller organisms (Gillooly et al. 2002, Hillebrand 2004, Soininen et al. unpubl.). Finally, we found a subtle tendency for organisms with higher trophic position to have shorter halving distances. This is consistent with the earlier finding of strong gradients in alpha diversity for organisms with high trophic position (Hillebrand 2004, Holt and Hoopes 2005).

We believe that the regression of similarity against distance unites several ecological phenomena, and thus provides an effective approach for illustrating the spatial turnover across sites. As our most parsimonious GLM models included a number of factors, rate of distance decay appears to be jointly controlled by number of factors. On the one hand, distance decay is a product of latitude, study extent and environment, and on the other hand it is a correlate of organism characteristics. Generally, this probably implies that communities are controlled both by niche-based processes and neutrality, since both environment structuring and spatially contagious dispersal seem to affect the communities. This view is shared by many authors (Duque et al. 2002, Soininen et al. 2004, Vormisto et al. 2004, Cottenie 2005, Thompson and Townsend 2006, Jones et al. 2006), and the extent to which organisms are controlled by dispersal-driven assembly or local ecological determinism may be often linked to spatial extent of the study. Chave (2004) even stressed that the niche- and neutral processes are complementary also theoretically, given that the former refers to deterministic processes in species poor communities, and the latter to highly diverse assemblages emphasizing the role of stochastic processes in coexistence. Future studies addressing the relationships between community structure, environment and space should perhaps focus on decoupling distance and environment at multiple scales using more sophisticated sampling designs and analytical methods (Gilbert and Lechowicz 2004). A fruitful approach would be, for example, a simultaneous sampling of

multiple taxa at same localities to examine if among-organism variability in dispersal rates has major implications for the relationships between community and geographical distance and between community and environmental distance across taxa. This would provide interesting way to gauge the importance of dispersal against the strength of local constraints.

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