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ORIGINAL ARTICLE

Environment, dispersal and patterns of species similarity

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ABSTRACT

Aim The aim of this paper is to evaluate the combined effects of geographical distance and environmental distance on patterns of species similarity (similarity in species composition between sites), and to identify factors affecting the rate of decay in species similarity with each type of distance.

Location Israel.

Methods Data on species composition of land snails and land birds were recorded in 27 sites of 1 × 1 km scattered across a rainfall gradient in Israel. Matrices of similarity in species composition between all pairs of sites were computed and analysed with respect to corresponding matrices of geographical distance and rainfall distance (defined as the difference in mean annual rainfall between sites, and used as a measure of environmental distance). Mantel tests were applied to determine the correlation between species similarity and each type of distance. Factors affecting the decay in species similarity were investigated by comparing different subsets of the data using randomization tests.

Results Both rainfall distance and geographical distance had negative effects on species similarity. The effect of rainfall distance was statistically significant even after controlling for differences in geographical distance, and vice versa. The per-unit effect of rainfall distance on species similarity decreased with increasing geographical distance, indicating that the two types of distances interacted in determining the similarity in species composition. Snails showed a higher rate of decay in species similarity with geographical distance than birds, and large snails showed a higher rate of decay than small snails, which are better passive dispersers. The per-unit effects of both rainfall distance and geographical distance on species similarity were higher in the desert region than in the Mediterranean region. Analyses focusing on a grain size of 10 × 10 m showed a lower similarity in species composition and a lower rate of decay in species similarity with rainfall distance than analyses carried out at a grain size of 1 × 1 km.

Main conclusions Patterns of similarity in species composition are influenced by the combined effects of environmental variation, the position of the area along environmental gradients, the dispersal properties of the component species, and the scale (both spatial extent and grain size) at which the patterns are examined.

Keywords

Beta diversity, birds, environmental distance, geographical distance, grain size, Israel, land snails, Mantel test, species turnover, scale.

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INTRODUCTION

Explaining patterns of spatial variation in species composition is a major challenge facing ecologists. While many studies have focused on patterns of species richness and their causal factors, the spatial change in species composition has received far less attention (but see Harrison *et al.*, 1992; Cody, 1993; Nekola & White, 1999; Condit *et al.*, 2002; Veech, 2005).

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Spatial turnover in species composition, or beta-diversity following Cody (1993), is, however, a major determinant of species diversity at the regional scale. Thus, any attempt to understand the structure of ecological communities must take into account the role of species turnover and the factors that influence it. In a seminal paper on the analysis and interpretation of spatial patterns in species composition, Nekola & White (1999) proposed that factors affecting the spatial structure of ecological communities can be studied by analysing the degree of similarity in species composition between sites ('species similarity'). They argued that species similarity decreases with increasing distance between sites, and that this 'distance decay' reflects the combined effects of two fundamental factors: niche relationships, and dispersal processes. Niche relationships produce a decay of species similarity with geographical distance because environmental conditions are always spatially autocorrelated, so that nearby sites tend to be more similar in their environmental conditions than distant sites (Legendre, 1993). The spatial decay in environmental similarity leads to a corresponding decay in species similarity.

Dispersal processes produce a distance decay in species similarity because dispersal distances are always limited in space, so that at any given time not all species detect (and thus, occupy) all habitats (Shmida & Ellner, 1984; Fleishman *et al.*, 2001). Hence, distant sites may show low species similarity even though they share the same environmental conditions (Primack & Miao, 1992). On the other hand, the spatial mass effect (*sensu* Shmida & Whittaker, 1981) may cause species to occur in unsuitable habitats by dispersal from nearby, suitable habitats, and thus increase the degree of species similarity over short distances. Dispersal limitation and the mass effect produce spatial autocorrelation in species composition, and hence a decay of species similarity with geographical distance (Nekola & White, 1999; Bell, 2001; Hubbell, 2001).

Since the publication of Nekola & White (1999), an increasing number of studies have documented patterns of distance decay in ecological communities (e.g. Spencer *et al.*, 2002; Tuomisto *et al.*, 2003; Qian *et al.*, 2005). Almost all of these studies have focused on plant communities, however, and the degree to which the observed patterns can be applied to animal communities remains unclear. Furthermore, in spite of some indications that the effect of geographical distance on species similarity depends on the magnitude of environmental heterogeneity (Cody, 1993; Condit *et al.*, 2002), no study has tested whether and how geographical distance interacts with environmental distance in determining patterns of species similarity. In addition, while many studies have documented patterns of decay in species similarity with geographical or environmental distance, factors affecting the rate of decay in species similarity have rarely been tested (although see Ferrier *et al.*, 1999; Tuomisto *et al.*, 2003). Another question that has not been examined in previous studies is whether patterns of distance decay depend on the position of the area along environmental gradients. For example, since the relative importance of water as a limiting factor decreases from desert to more mesic ecosystems, the position of a region along the rainfall gradient may influence the degree to which local variation in rainfall is 'translated' into variation in species composition. Such dependence, if it occurs, may complicate the interpretation of observed patterns of distance decay and the comparison of patterns obtained from different ecological systems.

In this research we test a set of predictions concerning the combined effects of geographical distance and environmental distance on species similarity using field data on the distribution of land snails and land birds along a rainfall gradient in Israel. We used the difference in mean annual rainfall between sites (rainfall distance) as a measure of environmental distance because of its importance in determining the regional distribution of land snails (Kadmon & Heller, 1998) and birds (Shirihai, 1996; YomTov & Werner, 1996) in Israel. By focusing on taxa representing extremely low vs. high vagility we attempted to evaluate the degree to which dispersal ability is important in determining the decay in species similarity with geographical distance.

Specifically, we tested the following predictions.

1 Species similarity should decay with both rainfall distance and geographical distance.

2 The per-unit effect of rainfall distance on species similarity (the change in species similarity per unit change in rainfall distance) should decrease with increasing geographical distance. This interaction is expected because species similarity between geographically close sites may vary from low to high values depending on the similarity in rainfall conditions, whereas species similarity between geographically distant sites is limited by dispersal, and is therefore expected to be low independently of rainfall conditions.

3 Rainfall distance should have a stronger per-unit effect on species similarity in desert regions than in the Mediterranean region.

4 The decay of species similarity with geographical distance should depend on the dispersal ability of the species. Specifically, snails should show a steeper decay of species similarity with geographical distance than birds. Moreover, since passive dispersal in land snails is a major determinant of long-range dispersal and is negatively related to shell size (Hausdorf, 2000), large snails should show a steeper decay in species similarity than small snails.

5 Because different environmental factors operate at different spatial scales, patterns of distance decay should depend on the grain size at which they are analysed. In general, analyses based on data from small grain sizes (e.g. 10 × 10 m) should show a weaker correlation between species similarity and rainfall distance than analyses based on larger grain sizes, because increasing the grain size averages the local stochastic variation in species composition and the related variability caused by fine-scale vegetation and edaphic heterogeneity.

METHODS

Field sampling

The study system was confined to areas having more than 90% natural vegetation and 90% carbonate rocks (a total of

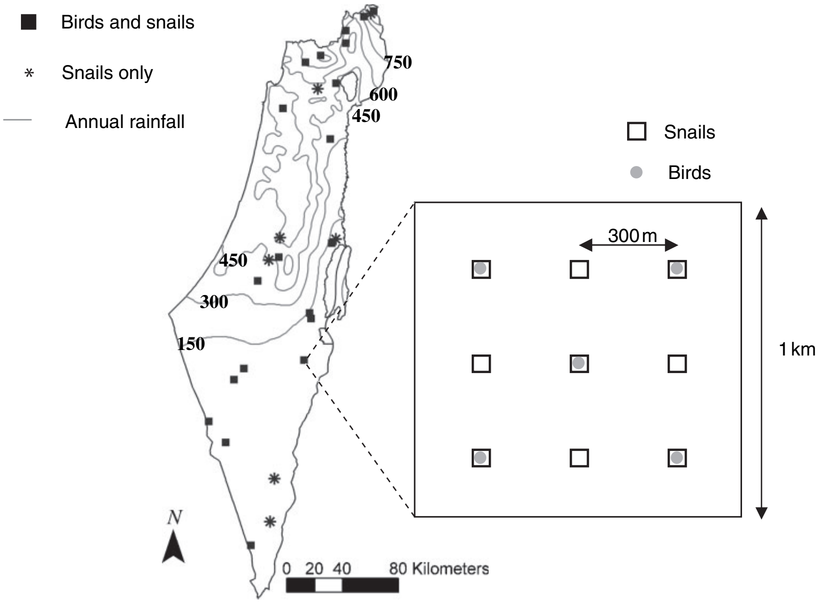

Figure 1 The study area, the locations of the study sites, and their sampling design. The squares on the map represent the 20 sites sampled for both snails and birds. Asterisks represent sites sampled only for snails. Contours represent mean annual rainfall (mm). In the enlargement (a single site), squares represent the nine sampling plots searched for snails, and grey circles represent the five observation points used for bird sampling. The central plot of each site was used for the fine-grain (10 × 10 m) analysis of species similarity.

6600 km^2). The restriction of the study system to areas that were relatively uniform in their lithology and land use was enforced in order to control for potentially influencing factors that were beyond the scope of this study. Field sampling was carried out in 27 sites of 1 × 1 km covering the main climatic gradients of Israel (Fig. 1). The spatial distribution of the sites was determined using a novel computer application designed to maximize the spreading of the sampling sites within a two-dimensional space determined by rainfall distance and geographical distance, while minimizing the correlation between the two types of distances (Steinitz *et al.*, 2005). This procedure of site selection enabled us to optimize the separation of the effects of rainfall distance and geographical distance on species similarity.

The sites selected for the study were sampled in 2001–02. Each site was sampled for land snails using nine uniformly spaced plots of 10 × 10 m (Fig. 1). We located each plot in the field using topographical maps, orthophotos, and a Garmin 12XL GPS with a spatial accuracy of 12 m (Garmin International Inc, Olathe, Kansas). A searching time of 12 min was allocated for each plot. Since the activity of land snails in Israel is confined mainly to the winter period and is not constant throughout this period (Heller, 1988), our records were based on empty shells. Sampling was restricted to species with shells larger than 5 mm because accurate sampling of microsnails required a sampling effort that was not feasible at such scales.

Breeding land birds were sampled in 20 sites out of the 27 sites using point counts (Bibby *et al.*, 2000) at five regularly spaced points in each site (Fig. 1). At each point, birds seen or heard in a 10-min period within a 60-m radius were recorded. Each site was sampled twice during the main breeding season. The first sampling period was during the spring (March–April 2002) and the second was during the summer (July–August 2002).

The sampling effort (both number of plots and searching time) required for representing the snail and bird fauna was determined based on rarefaction analysis (Soberon & Llorente, 1993; Gotelli & Colwell, 2001) of data obtained from intensive preliminary sampling of several representative ecosystems (D. Rotem and O. Steinitz, unpublished data).

Data analysis

Similarity in species composition was quantified with the Jaccard index (Legendre & Legendre, 1998), which was suitable for the presence–absence data that were available in this study. This index determines the proportion of species shared by a pair of sites out of the total number of species present in these sites.

The species composition of land snails and breeding birds in each site was determined by pooling the data obtained from the relevant sampling plots (nine plots for snails and five plots for birds). The similarity in species composition between sites was summarized in two matrices, one for the snails and one for the birds. In one site sampled for snails no species were recorded. This site was omitted from the analysis because its similarity to all other sites was zero independently of the geographical or environmental distances between them (including this site in the analysis had a negligible effect on the results).

For land snails we also constructed a species similarity matrix using the data obtained from the central 10 × 10 m sampling plot of each site (Fig. 1). This matrix was compared with the corresponding site-level matrix in order to evaluate the effect of grain size on patterns of species similarity.

A matrix of rainfall distances (the absolute difference in mean annual rainfall between sites) was calculated from a raster map of mean annual rainfall that was constructed at a spatial resolution of 1 × 1 km using data from 475 rainfall stations (Kadmon & Heller, 1998). A corresponding matrix of geographical distances was computed based on the geographical coordinates of the site centres. These matrices were used as explanatory variables for the analyses at both grain sizes (10 × 10 m and 1 × 1 km).

The statistical significance of the relationship between species similarity and the two types of distances was tested using simple and partial Mantel correlations. Mantel tests were used because values in distance/similarity matrices are not independent. P values were calculated using Monte Carlo randomizations of the response variable (species similarity matrix unfolded to a vector). The analyses were applied using the R-package 4.0 program (Casgrain & Legendre, 2000). The results of these analyses enabled us to test the prediction that species similarity decreases with both geographical distance and rainfall distance (prediction 1).

Predictions 2 to 5 were tested by subdividing the data into subsets representing different sites or different species categories, and testing for differences in the rate of decay in species similarity with geographical or rainfall distance between the relevant subsets. These analyses were performed using randomization tests for differences between slopes of regression models (Nekola & White, 1999). First, species similarity values of the two data sets compared were rescaled to a common mean. Then, the species similarity value for each pair of sites along with the corresponding distance was randomly reassigned to one of the two data sets. After this randomization had been carried out, linear regressions were applied to determine the slope of the species similarity function for each of the randomized data sets, and the absolute value of the difference between the two slopes was determined. This procedure was repeated 999 times. The difference between the slopes of the original data sets (true assignments) was also calculated and compared with the distribution of the differences between the slopes of the 999 randomized data sets in order to determine its significance level.

The interaction between the effects of geographical distance and rainfall distance (prediction 2) was tested by classifying pairs of sites into two groups based on the geographical distance between them. One group included pairs of sites 0–200 km apart, and the other group included sites 200–400 km apart. For each group, species similarity was regressed against rainfall distance, and the difference between the slopes of the two regression models was tested using the randomization test. Separate tests were performed for snails and birds.

The effect of position along the rainfall gradient (prediction 3) was tested by classifying the sampling sites into desert sites (mean annual rainfall < 200 mm) and Mediterranean sites (350–1000 mm rainfall). Differences between the two climatic regions in the decay of species similarity with both geographic distance and rainfall distance were tested separately for snails and birds.

The effect of dispersal ability on the rate of decay in species similarity (prediction 4) was evaluated using two types of comparisons: snails vs. birds, and large snails (shell diameter > 10 mm) vs. small snails (shell diameter < 10 mm). A threshold value of 10 mm was used because this was the median shell diameter of the species sampled in this project.

The effect of grain size on species similarity (prediction 5) was tested using the snail data, by comparing the degree of similarity between sites (grain size of 1 × 1 km) with the degree of similarity between the central plot of each site (grain size of 10 × 10 m). The same geographical coordinates and rainfall values were used to characterize the sites and their central plots. Randomization tests were applied to evaluate whether differences in grain size influenced the decay of species similarity with rainfall distance and geographical distance.

RESULTS

In total, 50 snail species were recorded in 27 sites. The mean number of snail species per site was 8.44 (range 0–15 species). For birds, the corresponding figures were 79 species at 20 sites, with a mean of 16.5 species per site (range 2–35 species).

The effect of rainfall distance and geographical distance

Species similarity between sites decreased significantly with both rainfall distance and geographical distance for snails and birds (Table 1a). This result was consistent also for the plot scale (10 × 10 m) tested in snails (Table 1a). A significant negative effect of rainfall distance on species similarity was maintained after controlling for the effect of geographical distance between sites (Table 1b). Similarly, the negative effect of geographical distance on species similarity was statistically significant after controlling for the effect of rainfall distance in all analyses (Table 1b). These results were consistent for both snails and birds.

The interaction between rainfall distance and geographical distance

Sites at distances of < 200 km apart showed a steeper decay of species similarity with rainfall distance than sites separated by more than 200 km (Table 2). This interaction between the effects of geographical distance and rainfall distance was highly significant for both snails and birds (Table 2). A detailed examination of the combined effects of rainfall distance and geographical distance on species similarity revealed a gradual trend of decrease in the per-unit effect of rainfall distance on species similarity with increasing geographical distance (Fig. 2).

The effect of position along the rainfall gradient

The rate of decay in species similarity with rainfall distance was higher in the desert region than in the Mediterranean region (Fig. 3). The decay of species similarity with geographical distance was also higher in the desert region (Fig. 3). Both effects were statistically significant for both snails and birds (Table 3).

Table 1 Results of Mantel correlations between species similarity, rainfall distance and geographical distance. Analyses were carried out for birds at grain size of 1 × 1 km and for snails at grain sizes of both 1 × 1 km and 10 × 10 m. Analysis of the 10 × 10 m grain size was based on the species data obtained from the central 10 × 10 m plot of each site (Fig. 1) using the same coordinates and rainfall values as used for the 1 × 1 km grain size. (a) Simple correlations. (b) Partial correlations (the effect of each distance tested while controlling the effect of the other distance)

Group	Grain size	Explanatory variable	Mantel *r*	*P* value
(a)				
Birds	1 × 1 km	Rainfall distance	−0.579	< 0.001
Birds	1 × 1 km	Geographical distance	−0.559	< 0.001
Snails	1 × 1 km	Rainfall distance	−0.727	< 0.001
Snails	1 × 1 km	Geographical distance	−0.639	< 0.001
Snails	10 × 10 m	Rainfall distance	−0.578	< 0.001
Snails	10 × 10 m	Geographical distance	−0.468	< 0.001

Group	Grain size	Explanatory variable	Control variable	Mantel *r*	*P* value
(b)					
Birds	1 × 1 km	Rainfall distance	Geographical distance	−0.363	< 0.001
Birds	1 × 1 km	Geographical distance	Rainfall distance	−0.318	0.005
Snails	1 × 1 km	Rainfall distance	Geographical distance	−0.562	< 0.001
Snails	1 × 1 km	Geographical distance	Rainfall distance	−0.376	0.005
Snails	10 × 10 m	Rainfall distance	Geographical distance	−0.423	< 0.001
Snails	10 × 10 m	Geographical distance	Rainfall distance	−0.189	0.011

Table 2 Effect of distance between sites (< 200 km vs. > 200 km) on the slope of species similarity against rainfall distance. *P* values of differences between slopes were determined using one-tailed randomization tests based on 999 permutations

Group	Distance between sites	Slope	*P* value
Birds	< 200 km	−0.00057	< 0.001
	> 200 km	−0.00011	
Snails	< 200 km	−0.00039	< 0.001
	> 200 km	−0.00008	

The effect of dispersal ability

Species similarity in snails decreased with geographical distance at a higher rate than in birds (Fig. 4a). A classification of the snail fauna into small vs. large species indicated that large snails were characterized by higher decay in species similarity with geographical distance than small snails (Fig. 4b). Both patterns (snails vs. birds and large snails vs. small snails) were statistically significant (Table 4) and also occurred when analysing separately the desert data set and the Mediterranean data set (not shown). Further tests showed that the correlation between geographical distance and species similarity was statistically significant for both large snails ($r = -0.642$, $P < 0.001$) and small snails ($r = -0.370$, $P < 0.001$). However, when the analyses were corrected for differences in rainfall distance (using partial Mantel tests) the correlation of species similarity with geographical distance was highly significant for large snails ($r = -0.4068$, $P < 0.001$) but not significant for small snails ($r = -0.056$, $P > 0.05$).

The effect of grain size

Analysis of the snail data indicated that the decay of species similarity with rainfall distance was lower at the plot scale (grain size 10 × 10 m) than at the site scale (grain size 1 × 1 km) (Table 5). However, when the sites were classified into desert vs. Mediterranean sites, only the latter sites showed a statistically significant effect of grain size on the rate of decay in species similarity with rainfall distance (Table 5). Moreover, species similarity among plots (the smaller grain size) in the Mediterranean region was relatively low and uniform independently of rainfall distance (Fig. 5). In contrast, at the site level (the larger grain size) species similarity was negatively related to rainfall distance, although the slope of the decay was lower than that obtained for the desert region. These results indicate that grain size interacted with the position of the area along the rainfall gradient in determining the decay of species similarity with rainfall distance. The average level of similarity in species composition between plots was lower than the corresponding similarity between sites in both the desert and the Mediterranean regions (Fig. 6).

DISCUSSION

Our results indicate that both rainfall distance and geographical distance were important in determining patterns of species similarity among the study sites. However, as we predicted, the quantitative patterns of similarity in species composition were not uniform, and were influenced by properties of the species, the environment, and the scale at which the data were analysed. Below we discuss these patterns with respect to our predictions.

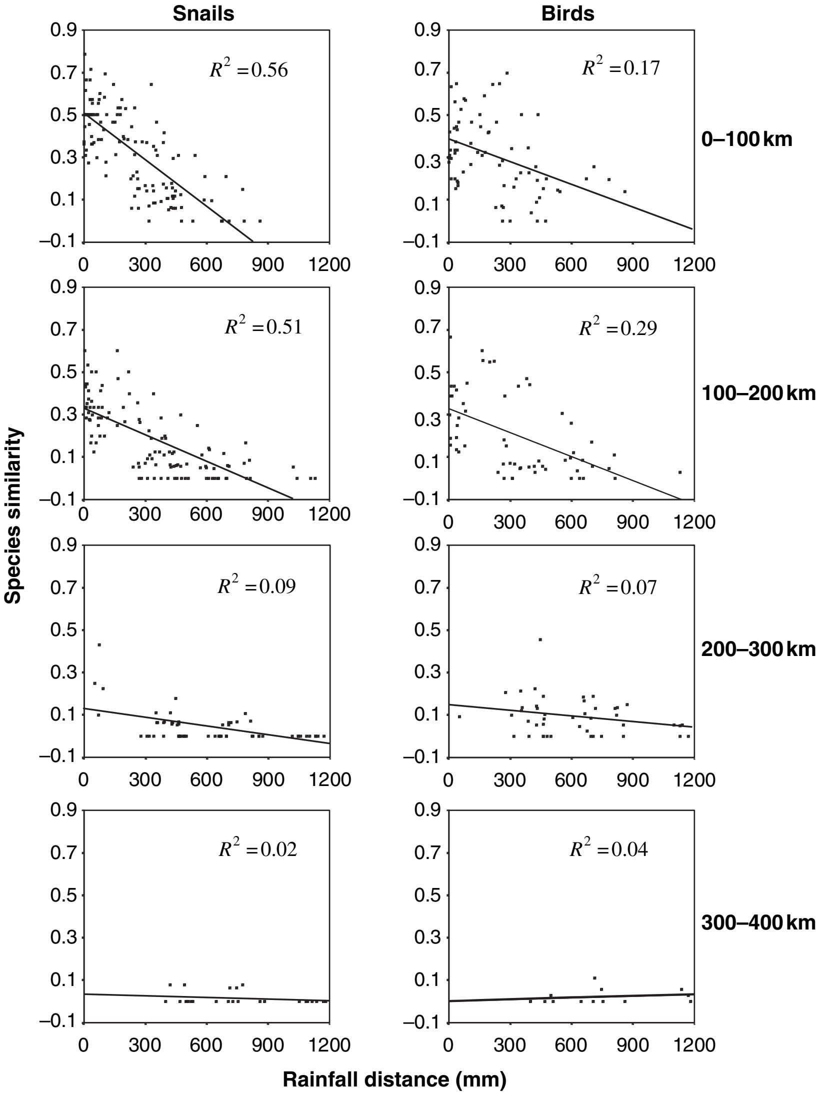

Figure 2 Effect of rainfall distance on species similarity for various categories of geographical distance (0–100, 100–200, 200–300 and 300–400 km). Each point represents a pair of sites. Analyses were carried out for snails and birds at a grain size of 1 × 1 km. Lines describe trends fitted by linear regression.

The effect of rainfall distance and geographical distance

Both rainfall distance and geographical distance had statistically significant effects on the species similarity of snails and birds. The effect detected for rainfall is consistent with results from previous studies focusing on regional variation in the composition of land snails (Kadmon & Heller, 1998) and birds (YomTov & Werner, 1996) in Israel. While such responses are not surprising considering the magnitude of variation in rainfall within the study area (32–1238 mm), our study indicates that these effects are highly significant also after controlling for spatial correlation in rainfall conditions.

In previous studies, spatial correlation in environmental conditions such as rainfall was mentioned as a major obstacle to exploring the independent effects of environmental vs. geographical distances on species similarity (Harrison *et al.*, 1992; Duivenvoorden *et al.*, 2002; Slik *et al.*, 2003; Qian *et al.*, 2005). In this study we coped with this difficulty in two ways: one related to the statistical analysis of the data and the second to the sampling design. Statistically, the effect of each type of distance was analysed using both simple and partial correlation analyses. This procedure enabled us to control statistically for the effect of geographical distance in testing faunal responses to rainfall distance and vice versa. The disadvantage of this approach is that it reduces the power of the statistical tests because all common effects are related to the control variable. Most previous studies on the combined effects of geographical distance and environmental distance on species similarity have, however, applied this approach (Jacquemyn *et al.*, 2001; Svenning & Skov, 2002; Tuomisto *et al.*, 2003; Green *et al.*, 2004).

A more efficient approach to coping with correlation between factors affecting spatial patterns of species composition is through the planning of the sampling design (Gilbert & Lechowicz, 2004). In this study we applied a novel methodology for sampling design that enabled us simultaneously to spread the sampling sites along a wide range of both rainfall distances and geographical distances while keeping the correlation between the two distances as low as possible

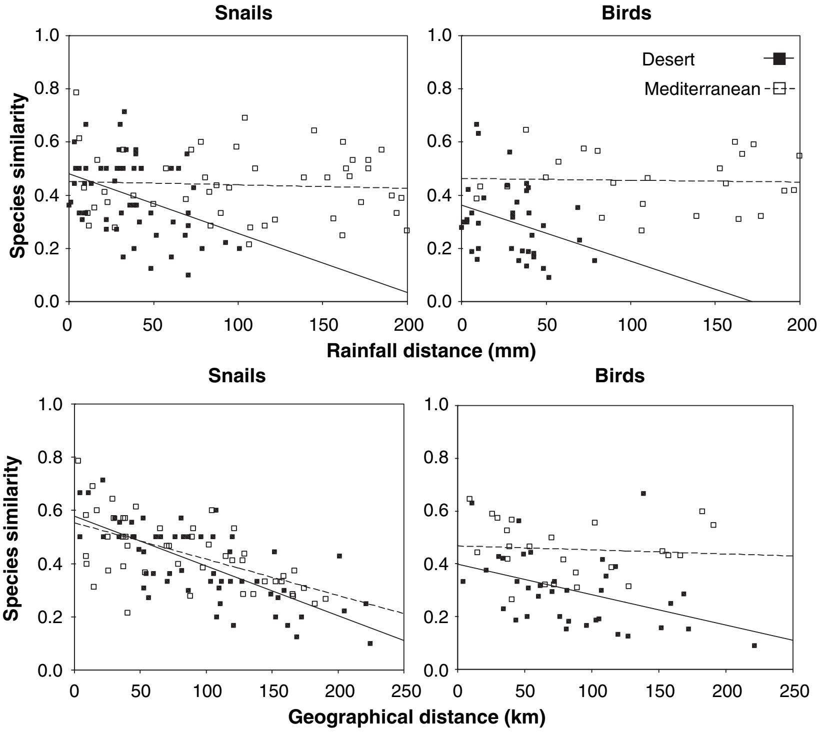

Figure 3 Differences between desert and Mediterranean regions in the effect of rainfall distance and geographical distance on species similarity. Analyses were performed at a grain size of 1 × 1 km. The desert data set is represented by closed squares and the continuous trend lines. The Mediterranean data set is represented by open squares and the dashed lines. Pairs of sites from the Mediterranean region with rainfall difference > 200 mm were excluded from the graph for better comparison with the desert sites (which were all within a rainfall distance of 200 mm). The general trend (slope and intercept) did not change when the Mediterranean data set was not limited in this way. Lines describe trends fitted by linear regression.

Table 3 Differences between desert (0–200 mm annual precipitation) and Mediterranean (350–1000 mm) regions in the slope of species similarity against rainfall distance and geographical distance. Analyses were performed at a grain size of 1 × 1 km. *P* values of differences between slopes were determined using one-tailed randomization tests based on 999 permutations

Group	Explanatory variable	Region	Slope	*P* value
Birds	Rainfall distance	Desert	−0.0021	< 0.001
		Mediterranean	−0.0004	
Snails	Rainfall distance	Desert	−0.0022	< 0.001
		Mediterranean	−0.0004	
Birds	Geographical distance	Desert	−0.0012	0.034
		Mediterranean	0.00010	
Snails	Geographical distance	Desert	−0.0019	0.037
		Mediterranean	−0.0013	

(Steinitz *et al.*, 2005). We believe that this selection of sampling sites contributed significantly to the detection of 'pure' rainfall effects in this study.

Although rainfall difference was important in structuring snail and bird communities in the study area, the geographical distance between sites also influenced species similarity in both groups. In a previous analysis we found that the effect of geographical distance on species similarity remained significant after controlling for a wide spectrum of other environmental factors, including various temperature indices, lithology, and vegetation (Steinitz *et al.* 2005). These findings support the hypothesis that dispersal processes were important in determining the patterns of species similarity observed in this study. It should be borne in mind, however, that a decay of species similarity with geographical distance can result from other, unmeasured environmental factors that are spatially autocorrelated.

Interaction between the effects of rainfall distance and geographical distance

'Pure' effects of geographical and environmental distances on species similarity have been documented in several previous studies (Cody, 1993; Ferrier *et al.*, 1999; Jacquemyn *et al.*, 2001; Svenning & Skov, 2002; Tuomisto *et al.*, 2003). However, our study provides the first evidence for an interaction of these two types of distances in their influence on species similarity. According to our results, the response of species similarity to rainfall distance is strongly scale-dependent (Fig. 2). In general, the effect of rainfall distance on species similarity weakens with increasing geographical distance. This finding indicates that the results of studies investigating the effects of environmental distances on species similarity (e.g., Duivenvoorden *et al.*, 2002; Potts *et al.*, 2002; Horner-Devine *et al.*, 2004; Qian *et al.*, 2005) can be influenced by the spatial extent of the area within which the analysis is carried out.

Several previous studies provide indirect evidence for interactions between the effects of environmental distance and geographical distance as determinants of species similarity. For example, Cody (1993) showed that the rate of spatial turnover in bird species composition varied between territories in Australia, and attributed this variation to underlying differences in the magnitude of habitat heterogeneity. Nekola & White (1999) attributed differences in rates of decay in

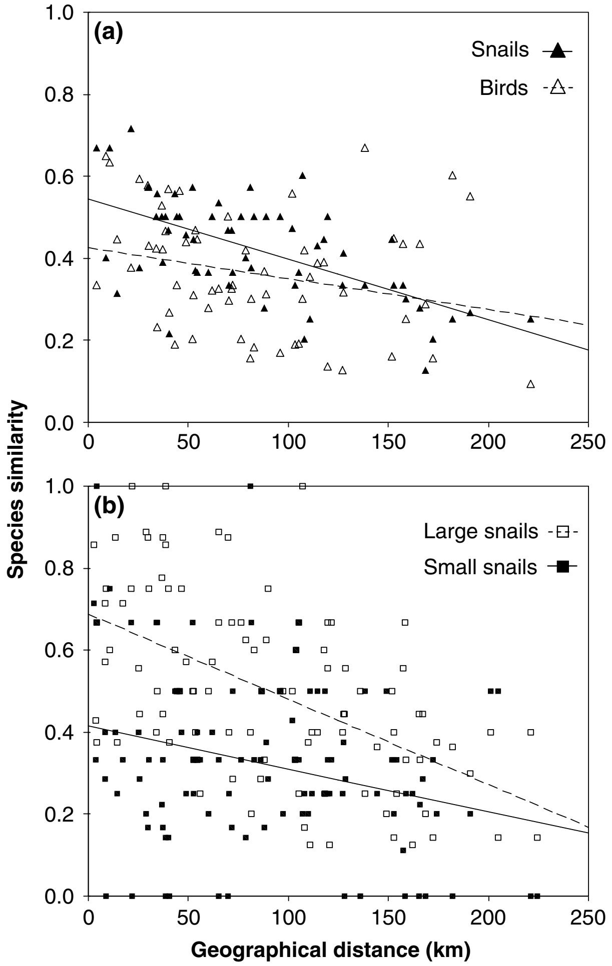

Figure 4 Differences between (a) birds and snails, and (b) large snails and small snails in the effect of geographical distance on species similarity. In (a) snails are represented by closed triangles and a continuous line and birds by open triangles and a dashed line. In (b) large snails are represented by open squares and a dashed line and small snails by closed squares and a continuous line. Only pairs of sites with rainfall distance < 200 mm are shown, for compatibility with Fig. 3. Lines describe trends fitted by linear regression.

Table 4 Comparison of the slope of species similarity against geographical distance between birds and snails, and between large snails and small snails. *P* values of differences between slopes were determined using one-tailed randomization tests based on 999 permutations

Group	Slope	*P* value
Birds	−0.0011	0.038
Snails	−0.0013	
Small snails	−0.0007	< 0.001
Large snails	−0.0017	

Table 5 Effect of grain size (1 × 1 km vs. 10 × 10 m) on the slope of species similarity against rainfall distance. Separate analyses were carried out for the 'all' data set, the desert region, and the Mediterranean region. *P* values of differences between slopes were determined using one-tailed randomization tests

Data set	Grain size	Slope	*P* value
All	1 × 1 km	−0.0005	< 0.001
	10 × 10 m	−0.0003	
Desert	1 × 1 km	−0.0022	0.365
	10 × 10 m	−0.0025	
Mediterranean	1 × 1 km	−0.0004	0.027
	10 × 10 m	0.0001	

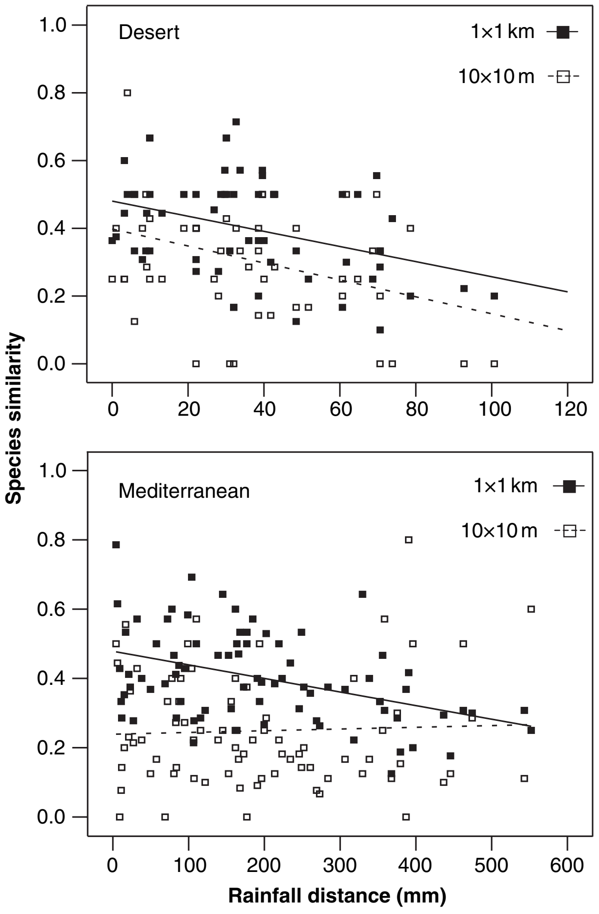

Figure 5 Effect of grain size (1 × 1 km vs. 10 × 10 m) on the decay of species similarity of snails with rainfall distance. Separate analyses were carried out for the desert and the Mediterranean regions. Data representing a grain size of 1 × 1 km are based on species composition at the site scale, and data for the grain size of 10 × 10 m are based on the species composition of the central plot in each site. Lines describe trends fitted by linear regression.

species similarity with geographical distance to differences in the steepness of the environmental gradients. Condit *et al.* (2002) observed a steeper decrease in plant species similarity with geographical distance in Panama rain forests compared with rain forests in Ecuador and Peru, and attributed this difference to a higher range of annual precipitation in Panama (Condit *et al.*, 2002; Ruokolainen & Tuomisto, 2002). These results are consistent with the hypothesis that environmental

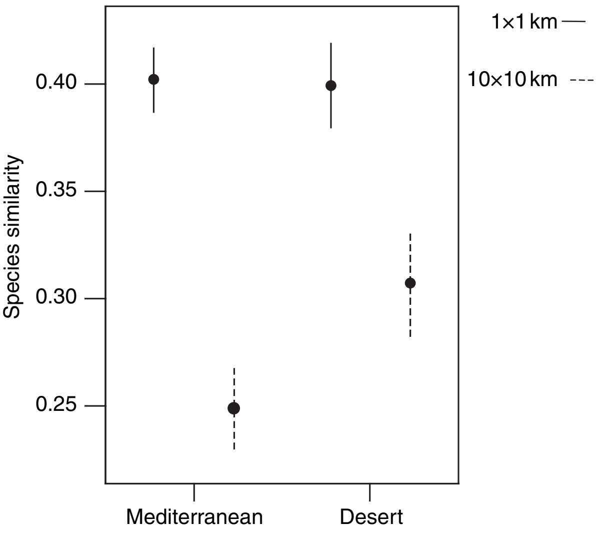

Figure 6 Differences in species similarity of snails between different grain sizes (1 × 1 km vs. 10 × 10 m) in the desert and the Mediterranean regions. Values represent average species similarity with standard error bars. Dashed error bars represent a grain size of 10 × 10 m and continuous error bars represent a grain size of 1 × 1 km.

distance interacts with geographical distance in determining patterns of species similarity.

The effect of position along the climatic gradient

The fact that species similarity decreased with rainfall distance at a higher rate in the desert than in the Mediterranean region supports the notion that patterns of species similarity may vary between regions according to their position along the climatic gradient. A possible explanation for this finding is that spatial variation in water availability is the main factor structuring ecological communities in desert areas, while other factors increase in their relative importance in more mesic areas. Independent support for this interpretation comes from an ordination analysis of snail distribution in Israel that was based on collection data (Kadmon & Heller, 1998). This study found that the rate of species replacement along the rainfall gradient was higher in desert areas than in more mesic areas. A similar pattern was documented for the flora of Israel (Kadmon & Danin, 1999), and for vegetation patterns in Kenya (Ogutu, 1996). In our study, desert areas differed from Mediterranean areas not only in the decay of species similarity with rainfall distance, but also in the decay of species similarity with geographic distance. This finding demonstrates that the position of a region along an environmental gradient may influence the magnitude of spatial turnover in species composition.

The effect of dispersal ability

The fact that groups of species with poor dispersal ability showed higher rates of decay in species similarity with increasing geographical distance compared with more vagile groups is consistent with the hypothesis that limited dispersal plays an important role in shaping patterns of regional variation in species composition (Bell, 2001; Hubbell, 2001). The fact that differences in the per-unit effect of geographical distance on species similarity were found in two independent comparisons (birds vs. snails and small snails vs. large snails) further supports this conclusion.

Previous studies found inconsistent relationships between dispersal ability and spatial turnover in species composition. For example, plants characterized by short-distance dispersal showed a higher rate of decay in species similarity with geographical distance than long-distance dispersers (Nekola & White, 1999; Tuomisto *et al.*, 2003); and ground-dwelling arthropods exhibited more pronounced patterns of species turnover with geographical distance than groups of vertebrates and plants characterized by higher mobility (Ferrier *et al.*, 1999). In contrast, Harrison *et al.* (1992) found no clear relation between rates of decay in species similarity with geographical distance and the dispersal characteristics of 15 groups of animal and plant species; and Poulin (2003) found that the rate of geographical decay in species similarity for parasite communities was not determined by host mobility. These contrasting results suggest that factors other than dispersal ability may be important in determining the decay of species similarity with geographical distance, a conclusion that is fully supported by our results.

In interpreting the differences obtained between snails and birds it should be noted that other ecological characteristics, such as differences in niche width or differences in the actual habitat grain perceived by the various species, may have contributed to the observed patterns. It should also be borne in mind that snails were sampled based on empty shells, which may represent records of more than one year, whereas bird records were collected over a time interval of less than one year. This difference may have introduced some bias to the observed differences in species similarity between the two taxa. We do not, however, expect this factor to affect the slope of species similarity against geographical or rainfall distance.

The effect of grain size

Nekola & White (1999) suggested that grain size might have a positive effect on the magnitude of species similarity between sites because small sites maintain only a subset of the species occurring in larger sites. Such a sampling effect can weaken the correlation between species similarity and geographical distance at relatively small grain sizes. Some support for this prediction was documented by Nekola (1999) for plant communities in north-east Iowa, although the effect of grain size was not consistent across habitats with different histories. The results obtained in our study are consistent with the prediction of Nekola & White (1999), and indicate that the average level of species similarity is positively related to grain size. The increase in species similarity with grain size can be a consequence of averaging local-scale variation caused by stochasticity in the occurrences of species, or local heterogeneity in environmental factors such as substrate and vegetation conditions.

The effect of grain size on the decay of species similarity with rainfall distance was influenced by the position of the area along the rainfall gradient (Fig. 5, Table 5). In the desert region, the decay of species similarity with rainfall distance was highly significant for both grain sizes, and there was no difference in the slope of the decay between the two grain sizes. In the Mediterranean region, only the larger grain size showed a significant effect of rainfall distance, and the difference between the two grain sizes was statistically significant (Fig. 5, Table 5). We relate this interaction to the fact that Mediterranean landscapes are more complex and exhibit a higher degree of habitat heterogeneity at small spatial scales. This fine-grain heterogeneity, which is caused by local disturbances and microscale variation in the structure of the vegetation (Naveh, 1975; Shoshany, 2000; Herrando *et al.*, 2003), increases the magnitude of spatial variation in species composition within sites and blurs the decay of species similarity with rainfall distance (Fig. 5). At larger grain sizes (e.g. at the site level), this local variation in species composition is averaged out, and rainfall distance becomes a significant determinant of species similarity, although its effect is still weaker than that observed in the desert area.

CONCLUSIONS

The overall results of this study indicate that geographical and environmental distances interact in determining patterns of species similarity, and that rates of decay in species similarity are influenced by the climatic characteristics of the region, the dispersal properties of the species, and the scale (both spatial extent and grain-size) at which the analysis is carried out. Together with previous results showing that the effect of geographical distance remains significant after controlling for differences in other environmental factors, these findings provide support for the hypothesis that niche relationships interact with dispersal processes in determining regional patterns of species composition.

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