CONSEQUENCES OF SPATIAL AUTOCORRELATION FOR THE ANALYSIS OF METAPOPULATION DYNAMICS

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Abstract. The importance of spatial and temporal autocorrelation for the processes occurring at many different scales has been pointed out in the last few years. Although the role of spatial pattern in models on metapopulation dynamics has recently been recognized, there is a lack of empirical studies accounting for the consequences of considering autocorrelation in these processes. Here, we show that the conventional statistical methods used for determining the factors controlling species population dynamics (species density, sex ratio, and extinction events) can be strongly affected by spatial autocorrelation. Under these circumstances, the use of a spatially explicit model is highly recommended in order to demonstrate the real factor controlling species population dynamics. Moreover, presenting erroneous conclusions concerning the real factors governing species population dynamics could have far-reaching consequences in the management and conservation of many endangered species.

Key words: metapopulation dynamics; spatial autocorrelation; spatial pattern; spatially explicit models; spatially implicit models; Timarcha lugens.

INTRODUCTION

How spatial heterogeneity and patchy habitat affect population dynamics and extinction risks has been one of the main questions in ecology during the last few decades (Levins 1970, Hanski and Gilpin 1997, Hanski 1999). Ever since Levins (1970) introduced the concept of the metapopulation, numerous empirical and theoretical studies have addressed this issue (see Hanski and Gilpin 1997, Hanski 1999, Hanski and Gaggiotti 2004). Although many metapopulation models have been developed, most are spatially implicit models, that is, the spatial location of the habitat patches is ignored (Lande et al. 2003). This occurs despite that, in most systems, nearby populations share more similarity than would be expected by chance (spatial autocorrelation; Legendre 1993, Legendre and Legendre 1998, Koenig 1999, Fortin and Gurevitch 2001). Therefore, metapopulation properties may depend on the spatial distribution of suitable habitats that could be subjected to spatial and temporal environmental autocorrelation (Hastings and Harrison 1994, Harrison and Bruna 1999). Indeed, an increase in the spatial scale of environmental autocorrelation increases the spatial scale of population synchrony, which in turn heightens extinction risk (Engen et al. 2002a, b, Pike et al. 2004). Moreover, spatial autocorrelation can affect the size of populations and prevent the recovery of locally extinct populations (Gonzalez and Holt 2003). Consequently, recent studies have pointed out the importance of using spatially explicit models when studying population dynamics (i.e., Hanski and Thomas 1994, Hanski and Gilpin 1997, Smith and Gilpin 1997, Bascompte and Solé 1998, Kendall et al. 2000, Lande et al. 2003).

Unfortunately, there is a lack of empirical studies accounting for the consequences of considering autocorrelation on the dynamics of metapopulation systems (Smith and Gilpin 1997, Marsh et al. 1999, Bohan et al. 2000, Trenham et al. 2001).

The factors determining extinction risk and species abundance have traditionally been explored in metapopulation systems by using multivariate parametric models. However, the use of these kinds of analyses when there is temporal or spatial autocorrelation entails statistical problems (Legendre 1993, Haining 2003). Indeed, one of the main assumptions in parametric analyses, the independence of the data, is violated (Legendre and Legendre 1998, Haining 2003). This provokes an error in the specification of degrees of freedom, which augments the probability of rejecting the null hypothesis and reduces the explanatory and predictive power of the models (Legendre and Legendre 1998, Haining 2003). There are many different approaches to incorporating space in ecological analyses, such as the trend surfaces analysis, spatial generalized least-squared or the spatial autoregressive models (Cressie 1993, Legendre and Legendre 1998, Lichstein et al. 2002, Haining 2003). Some of these detect only large-scale patterns, while others account for local spatial autocorrelations (Legendre and Legendre 1998, Haining 2003). Recently, Borcard and Legendre (2002) have proposed an improved method based on the computation of the principal coordinates of a matrix of
geographic neighbors among the sampling sites (PCNM). This method accounts for spatial patterns over a wide range of scales, from coarse-scale spatial trend to fine-scale autocorrelation (Borcard and Legendre 2002, Borcard et al. 2004).

In this paper, we test for spatial autocorrelation both in environmental variables and in population parameters for the metapopulation of Timarcha lugens (Coleoptera, Chrysomelidae), and we examine the consequences for our conclusions of using a spatially explicit analysis vs. implicit statistical tests.

**METHODS**

**Natural history of the system**

Timarcha lugens Rosenh. (Timarcha henceforth) is a high-altitude aperous beetle endemic to the Sierra Nevada mountains (southeastern Spain), occurring from 2400 to 3200 m above sea level. Active soon after snowmelt (late June at the study site) until the end of September, it is monophagous on Hormathophylla spinosa Küpfers (Cruciferae) as adults and larva, feeding on leaves, flowers, and fruits (for more details on Timarcha natural history, see González-Megías et al. [2004]).

The host plant, *H. spinosa*, is a long-lived stunted shrub inhabiting the high mountains of the western Mediterranean. As a consequence of *H. spinosa*’s patchy distribution in the alpine zone of the Sierra Nevada Mountains, the *Timarcha* population structure resembles that of a metapopulation, beetles inhabiting patches of the host plant connected by rare immigration events, with local extinctions occurring in some patches (González-Megías et al., in press).

**Study area**

The field work was conducted in the San Juan Valley (4 × 3 km, 37°4′ N, 3°22′ W; Fig. 1) from 2400 m to 3000 m altitude for five years (1998 to 2002). A total of 20 patches of the host plant were tagged (Fig. 1) and their position determined using a GPS (eTrex; Garmin, Olathe, Kansas, USA).

**Data collection**

We established two 10 × 2 m transects per *H. spinosa* patch to determine *Timarcha* density. These transects were not permanent and were assigned haphazardly every year. Transects were at least 2 m apart from each other. In each transect, we counted the number of beetles, recording the sex and stage (adult or larva). Patches where no beetles were found were visited periodically throughout the breeding season in order to ensure the absence of individuals. In each transect, the number of plants per transect was counted and their size estimated (measuring the height and two perpendicular diameters of the plants). To avoid differences in phenology among beetle populations, the censuses were conducted at the same phenological stage of the plant (between late June and early July).

Three descriptors of beetle populations were used for the analyses: (1) beetle density, which was calculated as the number of beetles per square meter; (2) extinction, which was defined as a binary variable (1 for populations that went extinct in at least one of the study years and 0 for those patches without any extinction event); and (3) sex ratio, which was the number of males divided by the number of females.

The following characteristics were estimated for each patch (see González-Megías et al. 2004 for a detailed description): (1) altitude; (2) patch area (in square meters); (3) river position (as a variable with three categories: left [patches located on the left bank of the river], right [patches located on the right bank of the river], and center [patches located between the two branches in the source of the river]), (4) aspect (sorted into three categories: flat, east-facing slope, and west-facing slope); (5) isolation (estimated in two ways: the distance to the nearest occupied patch and the mean distance to the three nearest occupied patches; because all the analyses gave the same results for both isolation measures, for brevity we present only the second measure in this study); (6) plant density (number of plants per square meter); and (7) average plant size per patch (in cubic centimeters; the heights and two perpendicular widths of the plants were measured, and
plant volume estimated using the formula of a hemisphere).

**Data analysis**

To investigate the putative factors explaining the among-patch differences in *Timarcha* population dynamics, we computed causal models using two methods. One was the d-sep test developed by Shipley (2000; DGRAPH, available online). This method was selected because it does not require large sample sizes and allows the use of binary variables (such as extinction). The second method was structural equation models (SEM, Proc SEPATH; Statistica version 6.0, Statsoft, Tulsa, Oklahoma, USA) with Monte Carlo procedures to avoid problems due to binary variables and low sample sizes. We hypothesized causal links among patch characteristics and each dependent variable, building a basic a priori analytical model. In this basic model, we introduced plant size and plant density as intermediate variables, and, as independent variables, the remaining patch characteristics (Fig. 2). River position, aspect, and extinction were included as dummy variables. After building this basic model, we considered a number of alternatives, competing nested models sharing the same causal structure but eliminating some of the paths. These nested models were built by removing alternative nonsignificant variables from the previous covariance matrix. To reject or fail to reject a model, we used the goodness of fit (for d-sep and SEM methods, using the relationship between $\chi^2$ and df) and three information criterion indices: Akaike Information Criterion, Schwarz’s Bayesian Criterion, and Browne-Cudeck Cross Validation index for SEM models (Rawlings et al. 1998, Johnson and Omland 2004). Path coefficients (partial regression coefficients) were obtained from Monte Carlo methods. Only the general values of the models obtained from the d-sep test are given in the results and Appendix.

Spatial autocorrelation in all the explanatory variables and *Timarcha* population descriptors was investigated with Moran’s I coefficient using the R package, version 4.0 (available online). Moran’s I behaves like a Pearson correlation coefficient and calculates the similarity between observations from pairs of locations for each distance class for each independent variable. The number of equidistant distance classes was calculated following Sturge’s rule ($N_{\text{classes}} = 1 + 3.31 \log n$). Regular Bonferroni corrections were made to determine whether there was significant spatial structure in the different explanatory and dependent variables. If autocorrelation was present in the dependent variables, a multiple regression model for each dependent variable was performed using all explanatory variables. Spatial autocorrelation was again tested for in the residuals obtained from the multiple-regression models. If no spatial autocorrelation remained, then the spatial pattern observed in the raw data could be explained by the spatial pattern observed in the explanatory variables (Legendre and Legendre 1998).

From the different methods available for including spatial components as independent variables, we used the method of principal coordinates of neighbor matrices analysis (PCNM) because it accounts for spatial patterns over a wide range of scales (Borcard and Legendre 2002, Borcard et al. 2004). This method creates a set of explanatory variables (called spatial base functions) that have structure at all scales encompassed by the data matrix. The spatial base functions are then included as explanatory variables in any multivariate statistical model. We used the software SpaceMaker2 (Borcard and Legendre 2004) to generate the set of spatial base functions. The PCNM analysis generated 11 PCNM variables for extinction and sex ratio (over 19 sites) and 12 PCNM variables for beetle density (over 20 sites). We performed step-wise regression analyses to select the set of PCNM base functions that were significant and explained some of the variation for each dependent variable. Only the subset of variables corresponding to the fine scale were selected to be included as explanatory variables (arbitrarily, the first four variables; see Borcard and Legendre 2002).

We repeated the SEM models described above, adding the spatial base functions for each dependent variable. We proceeded as above, accepting the most parsimonious submodel according to the four criteria described above. If any of the space variables was nonsignificant, it was excluded from the model in the same way as for other nonsignificant nonspatial variables.

Original data were log (for linear measurements) or angular transformed (for percentages) when necessary to normalize the data.

**RESULTS**

**The effect of space on environmental variables and *Timarcha* distribution**

Altitude, river position, patch area, plant density, and plant size were nonrandomly distributed in space and, at least for one of the distance classes, the correlations were significant after a Bonferroni correction. In addition, beetle density, sex ratio, and extinction events were spatially autocorrelated in the study area (Fig. 3). As shown in the correlograms, the correlations were positive and significant in the nearest distance classes and both negative and positive in the intermediate classes after Bonferroni correction (Fig. 3).

After multiple regression analysis, some significant autocorrelation persisted at least at one distance class for sex ratio, extinction, and plant size (Fig. 3), and no autocorrelation remained at any distance classes for beetle density or plant density (Fig. 3).
**Factors affecting Timarcha distribution**

**Beetle density.**—The best causal model explaining beetle density ($\chi^2 = 5.72$, df = 8, $P = 0.67$; Appendix) identified river position, plant size, area, and altitude as explanatory variables, although area was not significant (Fig. 2). In this model, beetle density was significantly higher in the center of the river than in patches located on either side of the river. In addition, beetle density was positively affected by altitude and plant size.

For beetle density, the best causal model with explicit spatial effect for beetle density ($\chi^2 = 11.78$, df = 12, $P = 0.46$; Appendix) did not differ significantly from the spatially implicit model, except for the space function, and the absence of area (Fig. 2). As in the
previous analysis, river position, plant size, and altitude were significantly related to beetle density, although the significance of altitude was stronger (Fig. 2).

**Sex ratio.**—The best causal model with implicit spatial effect ($\chi^2 = 4.39$, df = 8, $P = 0.82$; Appendix) included altitude, plant size, river position, and area (Fig. 2). In this case, sex ratio was negatively related to altitude and plant size, and the proportion of males was smaller on patches located in the centre of the river and in patches with larger plants.

The causal model with explicit spatial effect for sex ratio differed from the nonspatial model ($\chi^2 = 30.86$, df = 30, $P = 0.52$; Appendix). In this case, the best model was formed by isolation, area, plant size, altitude, isolation, and space (Fig. 2). However, area was not significantly related to sex ratio.

**Extinction events.**—The most parsimonious causal spatially implicit model for extinction ($\chi^2 = 0.453$, df = 4, $P = 0.97$; Appendix) included altitude, plant density, and area as explanatory variables (Fig. 2). The probability of extinction was higher in patches located at lower altitudes and with greater plant density. Although area was included in the model, the relationship with extinction did not prove significant.

The best spatially causal model with explicit spatial effect for extinction ($\chi^2 = 6.82$, df = 9, $P = 0.56$; Appendix) included as explanatory variables river position, isolation, plant size, and a spatial variable (Fig. 2). Extinction occurred mainly in patches located on the left bank of the river, where plants are in general of small size. Isolation was positively and significantly related to extinction, the probability of population extinction increasing with isolation. However, space explained most of the variation in plant size and extinction.

**Discussion**

Our data showed that several explanatory, causal, and dependent variables had a nonrandom spatial distribution. The use of spatially explicit analysis thus proves necessary because spatial patterns were observed both for explanatory and dependent variables (Legendre and Legendre 1998, Legendre et al. 2002, Lichstein et al. 2002, Diniz-Filho et al. 2003). Indeed, the statistical problem when using conventional parametric analysis in the presence of autocorrelation is more evident when autocorrelation occurs in both dependent and independent variables than when it occurs in only one variable (Legendre and Legendre 1998, Legendre et al. 2002, Lichstein et al. 2002).

There are many different mechanisms that may produce spatial patterns in species abundance and extinction (Legendre and Troussellier 1988, Legendre and Legendre 1998, Koenig 1999, Fortin and Gurevitch 2001, Haining 2003). Indeed, as Haining (2003) pointed out, similar patterns of spatial autocorrelation may
arise from different underlying mechanisms. The variability in environmental conditions, both in space and time, is one of the mechanisms producing spatial patterns (Legendre and Troussellier 1988, Koenig 1999, Fortin and Gurevitch 2001, Lande et al. 2003). In our case, although the study area is very small (no more than 3 km between the farthest patches) to assume differences in environmental conditions, the steepness of the valley, the substantial differences in altitude, and the potential influence of the river point to a climatic pattern with important effects in terms of population dynamics. In addition, a spatial structure can be generated because the process that generated the values is spatial, and produce autocorrelation in the data (Legendre and Legendre 1998). For example, population dynamics factors, such as the dispersal ability of individuals or the interaction with natural enemies, can also provoke spatial autocorrelation in populations (Legendre and Troussellier 1988, Koenig 1999, Fortin and Gurevitch 2001, Peltonen et al. 2002, Lande et al. 2003), and are often assumed to operate on a smaller spatial scale than environmental factors (Legendre and Legendre 1998). For example, in many tree species the pattern of seed dispersal, both by wind and animals, produces spatial autocorrelation in the tree population (Frost and Rydin 1999, Nathan et al. 2000). Similarly, low dispersal ability produces spatial autocorrelation in the use of ponds by some amphibian species, closer ponds being more similar in the number of immigrants than ponds that are farther apart (Marsh et al. 1999, Trenham et al. 2001). The limited dispersal ability of Timarcha (González-Megías et al., in press) may produce spatial autocorrelation in Timarcha populations.

Differences between spatially explicit and not spatially explicit models

Causal models with explicit spatial effects differed from causal models with spatially implicit effects for all dependent variables. First, the spatially explicit models differed in the relative importance of some of the variables, as found in other systems (Legendre and Troussellier 1988, Lichstein et al. 2002, Diniz-Filho et al. 2003, Borcard et al. 2004). This is, for example, the main consequence observed in the beetle density model after including the spatial base function. In addition, there were also differences in the number and identity of variables involved in each type of model. For instance, isolation was an important variable for sex ratio only in the spatially explicit model. This was even more evident for extinction, where isolation and plant size appeared as new variables in the spatial model whereas plant density and altitude disappeared from the model.

The implications of our results in metapopulation studies become more evident when the results from both types of analyses are compared with the predictions of metapopulation theory. There are several empirical studies and theoretical models based on the assumption that the main factors related to extinction risk are patch area and connectivity (Hanski 1999, Wilson et al. 2002, Hanski and Gaggiotti 2004). A decrease in the average patch area means an increase in isolation, which can reduce the amount of movement of individuals among patches (Hanski 1999). The role of isolation appears to be more vital in species with very low dispersal abilities, such as Timarcha (Thomas and Hanski 1997, Menéndez et al. 2002, Wilson et al. 2002). Surprisingly, although isolation did not prove to be an important explanatory factor for any of the dependent variables in the spatially implicit models, it was a good predictor of sex ratio and extinction events after controlling for spatial location.

The importance of habitat quality as a missing parameter affecting metapopulation dynamics has also been recently pointed out (Cowley et al. 2001, Summerville and Thomas 2001, Bradford et al. 2003). Because Timarcha depends entirely on its host plant, we would expect plant density or plant size to constrain its distribution. The models for extinction events differed in the relative importance of both variables, and while plant density was important only in the spatially implicit model, plant size appeared as a new significant variable in the spatial model. River position also appeared as an important explanatory factor determining extinction events, but only in the spatial model. The effect of river position could be a combination of resource availability and microclimatic conditions. Indeed, a similar effect of microhabitat on population extinctions has been observed in other species (Lima et al. 1996, Föraire and Solbreck 1997). The conservation of the Timarcha population would be very different depending on whether the results from the spatially implicit models or the spatially explicit models were used. The first one is focused on patches with high plant density whereas the second one is concentrated on plant size, isolation, and microhabitat (river position).

In summary, although the role of space affecting the functioning of ecological systems has been widely recognized in recent years in many disciplines (Legendre and Troussellier 1988, Brodie et al. 1995, Smith and Gilpin 1997, Koenig 1999, Badgley and Fox 2000, Bohan et al. 2000, Jetz and Rahbek 2001, Lichstein et al. 2002, Lande et al. 2003, Borcard et al. 2004), as far as we know, no empirical studies have applied spatially explicit analysis to detect the factors determining abundance, extinction, and occurrence of local populations in metapopulation systems. The findings reported in the present study clearly demonstrate that the inclusion of the space in the models can change our conclusions concerning the identity, nature, and importance of these factors. Furthermore, in addition to the consequences regarding statistical methods, the consideration of space as another factor in explanatory models can have vital implications for the management and conservation of species.
Reports


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APPENDIX

A table showing some of the structural equation models possible for each dependent variable is available in ESA’s Electronic Data Archive: Ecological Archives E086-178-A1.


