

Determinants of extinction-colonization dynamics in Mediterranean butterflies: the role of landscape, climate and local habitat features

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Summary

1. Many species are found today in the form of fragmented populations occupying patches of remnant habitat in human-altered landscapes. The persistence of these population networks requires a balance between extinction and colonization events assumed to be primarily related to patch area and isolation, but the contribution of factors such as the characteristics of patch and matrix habitats, the species' traits (habitat specialization and dispersal capabilities) and variation in climatic conditions have seldom been evaluated simultaneously.

2. The identification of environmental variables associated with patch occupancy and turnover may be especially useful to enhance the persistence of multiple species under current global change. However, for robust inference on occupancy and related parameters, we must account for detection errors, a commonly overlooked problem that leads to biased estimates and misleading conclusions about population dynamics.

3. Here, we provide direct empirical evidence of the effects of different environmental variables on the extinction and colonization rates of a rich butterfly community in the western Mediterranean. The analysis was based on a 17-year data set containing detection/nondetection data on 73 butterfly species for 26 sites in north-eastern Spain. Using multiseason occupancy models, which take into account species' detectability, we were able to obtain robust estimates of local extinction and colonization probabilities for each species and test the potential effects of site covariates such as the area of suitable habitat, topographic variability, landscape permeability around the site and climatic variability in aridity conditions.

4. Results revealed a general pattern across species with local habitat composition and landscape features as stronger predictors of occupancy dynamics compared with topography and local aridity. Increasing area of suitable habitat in a site strongly decreased local extinction risks and, for a number of species, both higher amounts of suitable habitat and more permeable landscapes increased colonization rates. Nevertheless, increased topographic variability decreased the extinction risk of bad dispersers, a group of species with significantly lower colonization rates.

5. Our models predicted higher sensitivity of the butterfly assemblages to deterministic changes in habitat features rather than to stochastic weather patterns, with some relationships being clearly dependent on the species' traits.

Key-words: biodiversity hotspot, effective precipitation, lepidoptera, monitoring scheme, occupancy dynamics, PRESENCE, spatial heterogeneity, species' guild

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Introduction

As a result of human pressure, many animal populations are today restricted to remnant natural and semi-natural habitat patches embedded in landscape matrices mostly unsuitable for their survival. Such populations, occupying a collection of habitat patches, may thus form metapopulations, the persistence of which often reflects a dynamic equilibrium of colonization and extinction events (Hanski 1999). These dynamic processes are of vital importance for the long-term survival of a species, and investigating the factors governing them is an important subject in ecology and a significant goal in the conservation of biodiversity.

Many butterfly species are known to occur in spatially structured populations that usually follow the classical metapopulation concept, making them good biological models to study extinction and colonization processes (Thomas & Hanski 2004). These dynamic processes are assumed to be primarily related to patch geometry (area and isolation), although in some metapopulation studies – including several on butterflies – area and isolation have performed poorly as predictors of site occupancy (Prugh *et al.* 2008). These and other studies have shown that the characteristics of the patches themselves should not be ignored, as they may have strong effects on occupancy patterns by modifying local survival and colonization rates (Thomas *et al.* 2001; Fleishman *et al.* 2002; Prugh *et al.* 2008; Oliver *et al.* 2010). Thus, environmental variables such as adult food resources, type of land cover and topography can significantly affect the dynamics of spatially structured butterfly populations. Topography, in particular, has often been ignored in most studies assessing occupancy dynamics, despite the importance of this variable for explaining local survival in butterfly populations (Weiss, Murphy & White 1988), its good performance at predicting species richness (Illán, Gutiérrez & Wilson 2010; Stefanescu, Carnicer & Peñuelas 2011) and forecasting future species' distributions under climate change scenarios (Luoto & Heikkinen 2008).

Likewise, due to the rapid response of butterfly populations and communities to the changing climate (Roy *et al.* 2001; Devictor *et al.* 2012), stochastic fluctuations in weather patterns (temperature and precipitation) may affect extinction and colonization patterns as well, either indirectly, through changes in local resource availability, or directly, by conditioning butterfly physiology or behaviour (Ehrlich *et al.* 1980; Piessens *et al.* 2009; Cormont *et al.* 2010).

Moreover, unlike oceanic islands, habitat patches within terrestrial ecosystems are not embedded within a homogeneous hostile matrix. It has been shown that factors such as the type of landscape surrounding a patch, together with the species' traits, may determine the permeability of the matrix for a given species and thus affect the colonization of unoccupied sites (e.g. Ricketts 2001; Opdam & Wascher 2004; Dover & Settele 2008; Lizée

et al. 2011). In fact, it may even be difficult to differentiate between patch and matrix when both contain resources that directly affect survival, maintenance and reproduction within metapopulations (Vanreusel & Van Dyck 2007; Dennis 2010). Therefore, as pointed out by Dennis (2010), it has become increasingly obvious in butterfly metapopulation studies that there is a need to consider other information about the matrix than the simple presence or absence of a species' larval host plant.

Given all the above considerations, identifying the most relevant environmental variables that are associated with patch occupancy and turnover is not an easy task, but it is still a priority to enhance the persistence of multiple species under current global change (Fleishman *et al.* 2002; Opdam & Wascher 2004). However, although different species may respond differently to changes in the same environmental variables, depending on their degree of habitat specialization or dispersal abilities, very few studies have focused on the extinction–colonization dynamics of whole communities (Krauss, Steffan-Dewenter & Tschardtke 2003) and, to our knowledge, this has never been attempted for a large number of coexisting butterfly species monitored over an extended time frame.

Most studies on patch-occupancy dynamics assume perfect detection of the species, overlooking the fact that a species may be present at a site and yet go undetected (false absences). Given the ambiguity of nondetections, it is important to account for detection errors in any study aimed at estimating the true state of occupancy and related parameters, as ignoring them may result in misleading model predictions and incorrect conclusions about a population (Moilanen 2002; Mackenzie *et al.* 2006). Thus, robust inference about occupancy dynamics can only be achieved by explicitly accounting for detection probability, such as in multiseason occupancy models, which enable direct estimates of these parameters when detection is imperfect (MacKenzie, Nichols & Hines 2003).

Here, we analysed species' records from the Catalan Butterfly Monitoring Scheme, a network of butterfly recording sites in north-eastern Spain that has provided occupancy data uninterruptedly since 1994. This region of the Western Mediterranean is an important centre of biodiversity (Medail & Quezel 1999) with high levels of butterfly species richness (Hawkins & Porter 2003), but over the last several decades, this and other parts of the Mediterranean basin have been subjected to major changes in land use or cover and most natural habitats have been lost to, for example, intensive agriculture, tree plantations, reservoirs and urbanization (Symeonakis, Calvo-Cases & Arnau-Rosalen 2007). Species' detection/nondetection data from multiple years were analysed using multiseason occupancy models to obtain local extinction and colonization rates and to assess the effects of several environmental variables (local topography, suitable habitat area, landscape permeability, weather patterns) and species traits (e.g. habitat specialization and

dispersal capabilities) on these parameters. For instance, we assumed that an increasing aridity may induce higher larval mortality and higher dispersal of adults (because of lack of nectar and oviposition resources; e.g. Piessens *et al.* 2009), increasing both extinction and colonization rates. Model construction followed this and other biological hypotheses, and results were examined across species and compared between species groups (defined by degree of habitat specialization and dispersal capabilities) to assess the influence of the species' traits on the performance of the predictors of occupancy dynamics. Our modelling approach, by explicitly including species detection probability, allowed us to control for false absences and make robust inferences about occupancy changes over time. Unlike previous work where the processes governing species' composition are inferred from observed patterns of species richness; here, we focus on the underlying dynamic processes that generate occupancy patterns.

Materials and methods

STUDY AREA, DATA SET AND VARIABLES MEASURED

We used species' detection/nondetection data obtained from transect counts between 1994 and 2010 in Catalonia and the Balearic Islands (north-eastern Spain), as part of the Catalan Butterfly Monitoring Scheme or CBMS (www.catalanbms.org). This monitoring programme is based on standardized weekly surveys of adult butterflies conducted along fixed routes during the flight season (30 weeks, from March 1 to September 26), when all species are available to be recorded. During each visit to a site, observers walk a fixed transect route of about 2 km in length, recording all butterflies seen within a 5-m corridor. Transects are divided into a number of different sections, each corresponding to a particular habitat type (see Van Swaay *et al.* 2008 for a summary of the standard methodology). Temporal and spatial heterogeneities in local abundances that affected the recordability of the species were corrected to some degree in the statistical analysis of our data (i.e. via the modelling of detection probabilities).

Given that not all transects in the network had been monitored each year of our study period, we selected those transects with ≥ 10 years of data (24 in the mainland and 2 in the island of Minorca, see Fig. S1). These sites were located at elevations ranging from 0 to 1650 m above sea level and encompassed a wide range of environmental conditions and natural habitats (e.g. from dry Mediterranean habitats to subalpine habitats). Vegetation composition, geographic features and meteorological conditions were measured in and around the monitoring sites to quantify: suitable habitat area, landscape permeability, elevation and topographic variability, and effective precipitation. Species appearing in fewer than 10 sites were excluded from our data, to ensure inferential strength in our analysis (Oliver *et al.* 2010), keeping a total number of 73 species (the more widespread ones). Also, to simplify data processing, weekly surveys were pooled into monthly surveys, leaving 7 sampling occasions per season instead of 30. For each species, we finally created a detection/nondetection data set containing 26 rows (number of monitoring sites) and 119 columns [product of the number of surveys \times number of seasons (years)] for statistical analysis.

SUITABLE HABITAT AREA

Botanic surveys conducted during the years 2000–2003 were used to quantify the vegetation composition at each monitoring site. The habitat composition of each section within a transect was characterized by classifying all vegetation types along the recording route into 17 broad habitat categories, following the CORINE Biotopes Manual (Moss & Wyatt 1994). Habitat preferences for each species had been previously determined following the approach of Oliver *et al.* (2010), using count data from all the CBMS network to calculate population densities (i.e. individuals/100 m transect) across the 17 habitat classes (see Stefanescu, Carnicer & Peñuelas 2011). Note that suitable habitats may include not only breeding habitat but also those habitats used for other purposes such as shelter, nectaring (i.e. a resource-based habitat view *sensu* Dennis 2010). Then, for any given species and site, we measured the area of suitable habitat in the 5-m corridor along the sampling route.

LANDSCAPE PERMEABILITY

In order to describe the landscape surrounding each of the monitoring sites, we examined the land cover composition in a 2 km buffer centred on each transect using the information contained in the Land Cover Map of Catalonia (MCSC), a high-resolution (0.5 m) and detailed (61 legend categories) thematic map compiled through photointerpretation of digitalized 1:5000 colour orthophotographs and developed by the Centre for Ecological Research and Forestry Applications (CREAF) in year 2007. Land cover categories were grouped into three major landscape components, following a similar approach as Lizée *et al.* (2012): a first class consisting of green surfaces containing natural vegetation and nonintensive cropland, a second class containing surfaces corresponding to bare soils and intensive cropland and a third class containing water and impervious surfaces (buildings, roads, parking areas). Then, we assigned a coefficient of permeability for butterfly dispersal to each class. We assumed that most butterfly species would disperse more easily through more vegetated and natural landscape matrices rather than those with more unvegetated or artificial components. Therefore, we assigned a coefficient of 1 (surfaces with the highest permeability to dispersal) to the 1st class of components in the landscape, a coefficient of 0.5 (surfaces with intermediate permeability) to the 2nd class, and a coefficient of 0 (impermeable surfaces) to the 3rd class. We then calculated the percentage of surface covered by these three major components in the landscape surrounding each transect and multiplied them by their corresponding coefficient. By summing these quantities, we were able to compute a site-specific index of landscape permeability, thus obtaining a measure of the functional connectivity of the landscape for multiple butterfly species.

TOPOGRAPHY

We used the Catalan Digital Elevation Model (MDEC), an altitudinal matrix of 30 m resolution (available at www.icc.cat), to obtain information on elevation and topographic metrics for each sampling site. Topographic slope values were calculated using the Spatial Analyst extension of software ARCGIS v. 9.3 ESRI. Local topographic variability was obtained by computing the standard deviation of slopes in a 1 km buffer around each transect.

ARIDITY

Meteorological data were obtained from EObs v. 5.0 (Haylock *et al.* 2008), a high-resolution (0.25×0.25 , approximately $25 \text{ km} \times 25 \text{ km}$) gridded data set produced using hundreds of stations in Spain over the period 1950–2011. This data set has been widely used for impact studies of regional climate change (e.g. Gottfried *et al.* 2012). For this study, monthly mean temperature and precipitation values for the EObs grids containing the sampling stations were used to compute an index of local effective precipitation (EP; Thornthwaite 1948) as the difference between precipitation and potential evapotranspiration ($EP = P - PET$), which is equivalent to an aridity index, with negative values indicating stronger aridity and positive values indicating wetter conditions.

To analyse the relationship between butterfly dynamics and climate, we defined the periods of the year when aridity could mostly affect extinction and colonization dynamics by examining each species' life cycle (see Appendix S1, Supporting Information). Thus, for each butterfly species and year, we computed the mean EP of the months assumed to be most critical for larval survivorship and the mean EP of the months corresponding to the adult flight period.

OCCUPANCY MODELS

Detection/nondetection data for each species were analysed using multiseason occupancy models in program PRESENCE 4.1 (Hines 2006). Multiseason occupancy models deal with data collected during repeated surveys conducted at multiple sites over an extended time frame (e.g. consecutive sampling periods or seasons) and allow the assessment of seasonal changes in species occupancy with emphasis on the underlying dynamic processes of extinction and colonization. In our case, these dynamics were modelled as functions of covariates, and we built multiseason models that included parameters for initial occupancy (Ψ_1), colonization (γ) and extinction (ϵ), in addition to probabilities of detection (p) (MacKenzie, Nichols & Hines 2003).

MODELLING OCCUPANCY DYNAMICS

We limited our model set to plausible *a priori* hypotheses about the processes underlying detection, colonization and local extinction, and predefined a set of 60 candidate models to investigate these dynamic processes rather than conducting exploratory analyses including all the various combinations of potential covariates (see Appendix S2 for a detailed description of the candidate model set and our prior hypotheses). Because initial occupancy was not of primary interest in our study and because it is only a starting point for the analysis of extinction and colonization dynamics, initial occupancy was never related to a covariate and treated as a free parameter, following Ferraz *et al.* (2007). Species-specific detection probabilities (p) were always expressed as a combination of site, and two survey-specific covariates that may affect the detectability of individuals, that is, the phenology of the species at the site and the observer conducting the survey. Phenology was introduced as a multiplicative function of month and elevation, given that factors such as the timing of the survey and the elevation of a site (a proxy of temperature) determine the peak of adult emergence (i.e. the peak of abundance of adult butterflies) and hence the species' detection at a given site. In addition, detection probability obviously depends on the skills of the

observer. To account for this effect, recorders were classified into three categories of increasing experience (from beginners with no previous experience to recorders with more than 3 years of experience in the network), and this categorical variable was included as an additive effect in the detectability function.

Colonization and extinction probabilities were modelled either as constant parameters or as functions of different combinations of up to four continuous environmental variables: suitable habitat area (hereafter 'habitat area'), landscape permeability, topographic variability (hereafter 'topography') and seasonal aridity or effective precipitation (hereafter 'EP'). For the modelling of colonization probabilities, we used the mean EP of the months corresponding to the adult flight period, whereas for the modelling of extinction probability, we used the mean EP of the months corresponding to the larval period (see also appendix S2). All these site covariates were normalized prior to the analysis. Topography was never used in the modelling of colonization probability, because in our *a priori* hypotheses, we considered that topography could only affect the extinction parameter by buffering local butterfly populations against climatic extremes (see appendix S2, Supporting Information).

MODEL SELECTION AND ASSESSMENT OF PREDICTOR VARIABLES

Once we ran our candidate model set for each butterfly species, we based model selection on the Akaike Information Criterion (AIC) and selected our best model as the one with the lowest AIC value. Models that differed in <2 points of AIC ($\Delta AIC < 2$) were considered as top-ranked models (statistically equivalent to the best model of the set).

For each covariate, we calculated the summed Akaike weight of all models that contained the respective variable as a measure of the support it received. The sum of model weights cannot exceed 1, and top-ranked models always show the highest values. Therefore, we considered that a covariate was well supported in our modelling when the obtained sum was >0.6 , an indicator that it was included in higher-ranked models more often.

The beta coefficients describing the relationship between each predictor and the response variable (extinction or colonization) were extracted from the highest-ranked model containing the covariate (the one showing the most important effects of a predictor, which may not always be among the top-ranked models of the set). We selected 1 high-ranked model per species to obtain unique beta coefficients and corresponding standard errors (SE) for each type of predictor–response relationship (mean beta coefficients computed from statistically equivalent higher-ranked models yielded similar values). Species for which these coefficients and their SE were not estimable were removed for further analyses (see below). Standard errors were used to compute an approximate 95% confidence interval of the slope parameter, to facilitate inferences about the modelled relationship.

We examined the proportion of species showing good/bad support for a specific covariate in their models and tested for differences between proportions by performing Chi-square and Fisher's exact tests. We also drew inferences based on results of higher-ranked models for all species and for species within ecological groups by asking whether slope parameter estimates were of the predicted sign more frequently than expected by chance alone using one-tailed z-tests. For example, we checked whether the estimated relationship between landscape permeability and colonization probability was more often positive than negative.

ECOLOGICAL GROUPS

Following Stefanescu, Carnicer & Peñuelas (2011), we assigned each butterfly species to one of four categories of increasing mobility, from 1 (species with very low dispersal ability) to 4 (species showing long-range seasonal migration). In the same way, each species was classified into a category of habitat specialization, from 1 (extreme habitat specialists) to 4 (extreme generalists), based on the Species' Specialization Index (SSI) by Julliard *et al.* (2006) (for its implementation using CBMS data see also Stefanescu, Carnicer & Peñuelas 2011). To ease comparisons between groups, all species were eventually pooled into 2 categories of dispersal and specialization, respectively: bad dispersers (the above defined dispersal categories 1 and 2, $n = 45$) and good dispersers (dispersal categories 3 and 4, $n = 28$), and habitat specialists (the above defined specialization categories 1 and 2, $n = 32$) and habitat generalists (specialization categories 3 and 4, $n = 41$).

Given their high dispersal capabilities, long-range migratory species should show the highest mean colonization rates, whereas the extinction risk of extreme habitat specialists should be highest due to their narrow habitat requirements. Species traits should also affect the performance of the different predictors of extinction and colonization dynamics. We expected topography and habitat area to be more important for bad than for good dispersers at reducing extinction risks, as rescue effects [*sensu* Brown & Kodric-Brown (1977)] may help out local populations of good dispersers more often. Variables such as EP, by inducing changes in dispersal behaviour, and landscape permeability, by influencing individual dispersal through the matrix, could be more important for modelling the colonization of bad dispersers. Finally, we also expected local habitat area to be a stronger predictor of both extinction and colonization rates in specialists than in generalist species.

Results

BEST MODEL STRUCTURES

The most parsimonious model for colonization (being among the top-ranked in 77% of species) was the one considering an additive effect of landscape permeability, habitat area and EP, closely followed by the model considering only additive effects of landscape permeability and habitat area (74% of species, see candidate model set in Appendix S2). The associations that appeared more often among the most parsimonious models for extinction were an interaction effect of both habitat area and landscape permeability (52%), and an additive effect of habitat area, landscape permeability and topography (48%). 95% of the species showed habitat effects of some kind (alone or in interaction/addition with other variables) in the top-ranked models for extinction probabilities.

EFFECTS OF COVARIATES ON EXTINCTION AND COLONIZATION PARAMETERS ACROSS SPECIES

Prior to the examination of the best predictors of extinction and colonization processes among species, we removed from our results those species where the time-constant

model (a model with constancy in extinction and colonization parameters, but time, observer and elevation effects in detectability) was among the most parsimonious models ($\Delta\text{AIC} < 2$), to make sure that we were always selecting species for which the inclusion of covariates significantly improved the description of occupancy dynamics in space and time.

Twelve species showed no evidence of any effect of environmental covariates on colonization probability (i.e. the time-constant model was the best structure describing colonization dynamics). For the remaining 61 species, landscape permeability was the best supported covariate, occurring in the top-ranked models of all of them, and most of the time co-occurring with habitat area, which also received good support in 52 species. EP was only well supported in 15 species (see Appendix S3 for detailed results on summed AIC weights and slope parameter estimates for all species). Permeable landscapes increased colonization probability for most species (38 of 53 species with estimable slope parameters; $z = 3.506$, $P = 0.001$), and habitat area had always a positive effect when selected as a good predictor of colonization (Fig. 1). Thus, transects containing larger surfaces of suitable habitat and surrounded by more permeable landscapes are more likely to be colonized by a large number of species. Of the subset of species for which it was selected as a good predictor, EP showed no evidence of more negative than positive effects on the colonization parameter (Fig. 1).

Seven species showed no evidence of any environmental variable affecting extinction probability, but in the remaining 66 species extinction was always best described as a function of an external covariate: habitat area was well supported in 63 species, followed by landscape permeability (34 species), local topography (25 species) and EP (10 species). Larger habitat area decreased the extinction risk of 55 of 63 species; of the remaining species, five had no estimable slope parameters and three species showed positive but not statistically significant slopes (Fig. 1). Increasing topographic variability decreased the extinction risk of 16 of 21 species with well-supported results and estimable slope parameters, and this proportion was significantly higher than that of landscape permeability (12 of 28 species; Fisher's exact test, $P = 0.023$). Increasing EP (lower aridity levels) decreased the extinction risk of only 3 of 10 species, but these relationships were not statistically significant. Thus, for many species, extinction risks will be lower in transects containing larger areas of suitable habitat, and for a subset of species, increased topographic complexity may further decrease their probability to become locally extinct.

COMPARISON OF EXTINCTION–COLONIZATION RATES BETWEEN ECOLOGICAL GROUPS

Species-specific extinction and colonization estimates (Appendix S4) obtained from the time-constant model allowed us to calculate summary statistics (Fig. 2) and to

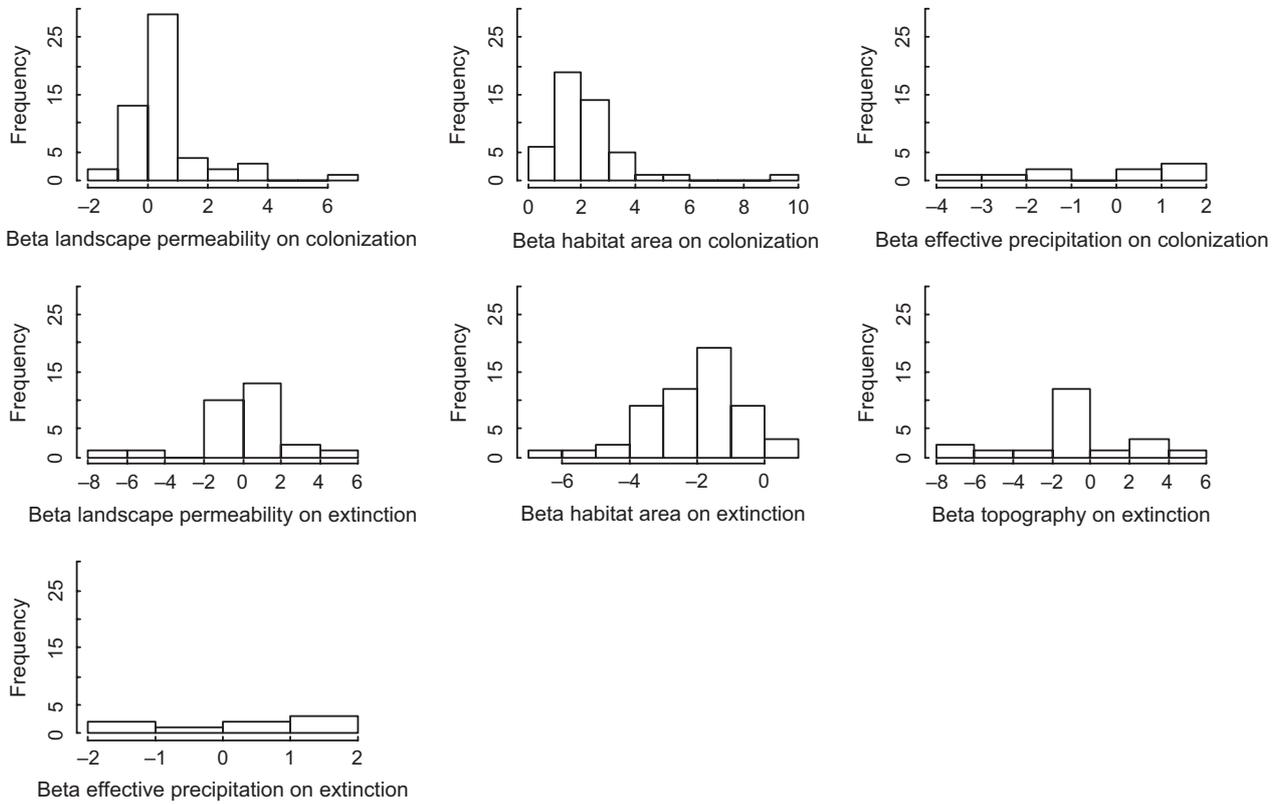


Fig. 1. Relationships between each predictor (environmental or site covariate) and the response variable (extinction or colonization). Beta coefficients defining the predictor–response relationships were extracted from the top-ranked models of species where the covariate received good support (summed Akaike weight >0.6). Large beta coefficients with no estimable standard errors were not included in the histograms.

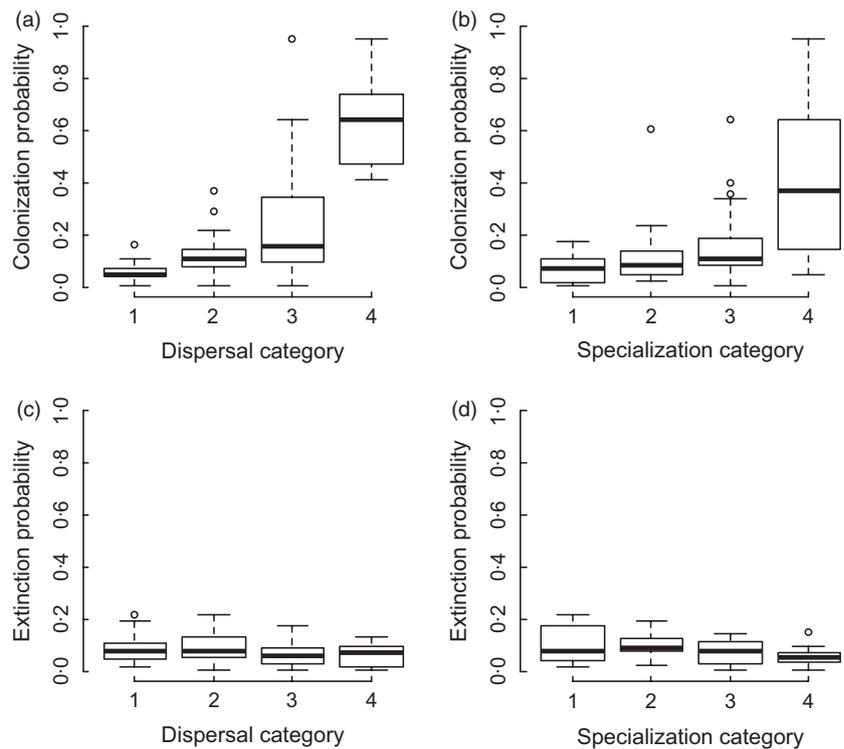


Fig. 2. Range of extinction and colonization estimates obtained for each dispersal and specialization category. Boxes and whiskers depict, in this order, the minimum value, lower quartile, median, upper quartile and maximum value of the observed distribution. Outliers are shown as white circles.

examine potential patterns across the different categories of dispersal and specialization. Results revealed similar extinction rates among dispersal and specialization categories

but significantly higher colonization probabilities of good dispersers ($n = 28$) compared with bad dispersers ($n = 45$; one-tailed z test: $z = 1.965$, $P = 0.025$).

CONTRASTING MODEL RESULTS BETWEEN GOOD AND BAD DISPERSERS

As predictors of colonization, landscape permeability received identical high support in both dispersal groups (21/21 good dispersers vs. 40/40 species of bad dispersers; proportions excluding species with no covariate effects on their colonization dynamics) and EP received better support in good than in bad dispersers (7/21 good dispersers vs. 8/40 species of bad dispersers; Fig. 3a), but this difference was not statistically significant ($\chi^2_1 = 0.699$, $P = 0.403$). Both groups showed similar proportions of positive relationships between colonization and the landscape variable (14/21 vs. 30/40; $\chi^2_1 = 0.152$, $P = 0.697$) and similar proportions of negative slopes for the EP variable (4/7 vs. 3/8; Fisher's exact test, $P = 0.619$).

As a predictor of extinction, topography performed significantly better in bad than in good dispersers (Fig. 3b; $\chi^2_1 = 4.257$, $P = 0.039$), with more negative ($n = 17$) than positive ($n = 3$) effects on extinction rates within the bad dispersers group ($z = 3.499$, $P = 0.001$). The habitat

variable received similar support as a predictor of extinction in both groups (Fig. 3b; proportions excluding species' with no covariate effects on their extinction dynamics), and there was no evidence of differences in the proportion of negative slopes between good and bad dispersers (22/22 vs. 38/41; Fisher's exact test, $P = 0.546$).

CONTRASTING RESULTS BETWEEN HABITAT SPECIALISTS AND GENERALIST SPECIES

Colonization probabilities increased with habitat area more often in specialist than in generalist species (Fig. 4a), and this difference was statistically significant (28/29 vs. 24/32; Fisher's exact test: $P = 0.027$). All predictors of extinction performed similarly between groups of specialization (Fig. 4b). Increasing habitat area did not reduce extinction risk of specialists more often, as we found no evidence of a higher proportion of negative slopes in specialists than in generalists (31/31 vs. 29/32; Fisher's exact test: $P = 0.238$).

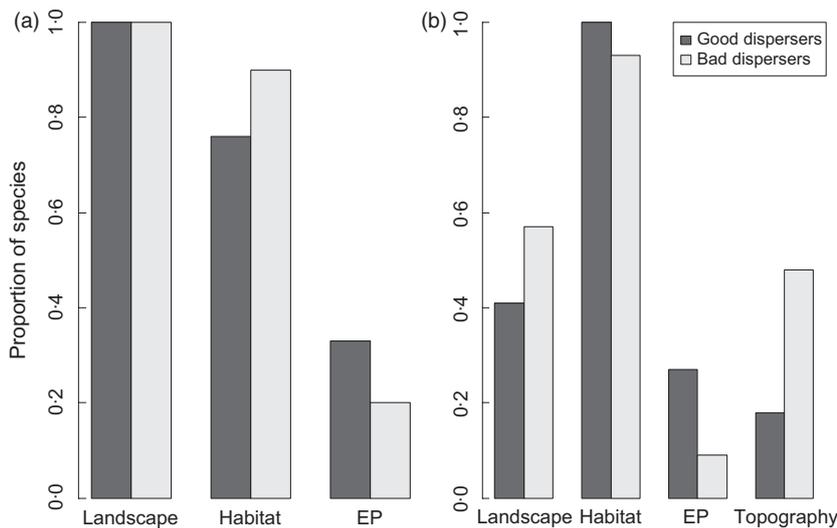


Fig. 3. Performance of the predictors of occupancy dynamics between dispersal categories (good vs. bad disperser species). A covariate is identified as a good predictor when its summed AIC weight is above 0.6. Panel (a) shows the proportion of species within each category where the covariate performs well as a predictor of colonization, and panel (b) shows the proportion of species where the covariate is a good predictor of extinction.

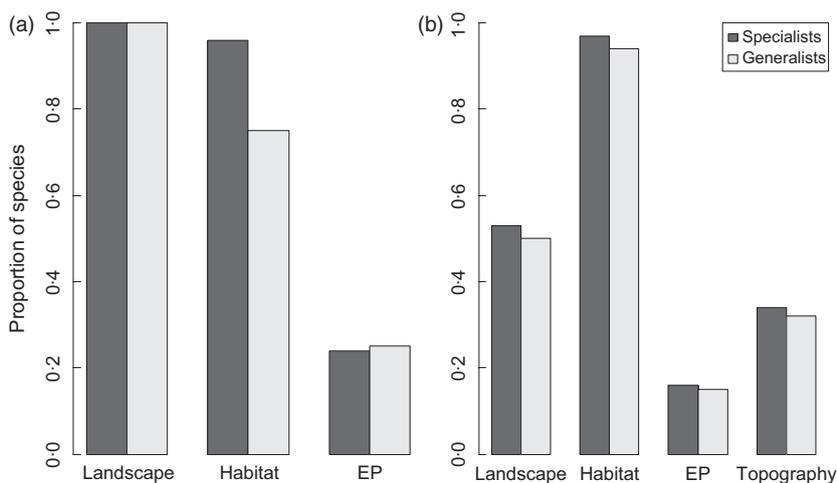


Fig. 4. Performance of the predictors of occupancy dynamics between specialization categories (specialist vs. generalist species). A covariate is identified as a good predictor when its summed AIC weight is above 0.6. Panel (a) shows the proportion of species within each category where the covariate performs well as predictor of colonization, whereas panel (b) shows the proportion of species where the covariate is a good predictor of extinction.

Discussion

By using an analytical framework that incorporated a diverse array of environmental variables and species characteristic traits, we explored the underlying processes determining occupancy in highly diversified Mediterranean butterfly assemblages. This approach provided, for the first time, reliable extinction and colonization rate estimates for a large number of coexisting species of butterflies, and shed light upon the factors influencing occupancy dynamics in a region with high environmental diversity and under strong human pressure.

Habitat area was the best predictor of extinction rates across species, with an expected decrease in local extinction risk of increasing areas. According to metapopulation theory, area is a proxy of population size: the larger the area, the larger the population and the lower the probability of extinction (Hanski 1999). However, because a too simplistic characterization of habitat patch quality-based solely on the presence-absence of the larval resources may overlook other characteristics of the habitat that are equally important (e.g. Thomas *et al.* 2001; Fleishman *et al.* 2002); here, we used a much broader – but still species-specific and resource-based definition (Dennis 2010). In this way, we believe that our measure of local habitat area reasonably estimates those portions of the recording transect that may sustain the highest population densities or at least those that provide the diversity and abundance of resources required for the survival of the species.

The local area of suitable habitat strongly affected colonization probability as well, and colonization rates always increased with habitat area. As pointed out by Jaquière *et al.* (2008), this positive effect might result from an active choice by dispersing individuals (implying the ability to target the sites containing more suitable habitat) or by a higher probability of successful settlement in larger recipient sites. In our study, habitat area did not perform better as a predictor of local colonization in good dispersers, despite their higher dispersal capabilities and hence increasing ability to detect tracts of suitable habitat in the landscape. Instead, significant differences were found between specialization categories, and colonization probabilities in specialists seemed to be more mediated by the local area of suitable habitat, suggesting that increasing area may be facilitating settlement of dispersing individuals.

Although the area of suitable habitat strongly affected colonization probability, the principal predictor of colonization across species was landscape permeability. Again, as expected, colonization probability increased with increasing permeability of the matrix surrounding the transect. Interestingly, however, the performance of this landscape variable was not affected by the species traits (note that this similar performance between ecological groups does not imply similar colonization probabilities, as good dispersers always showed significantly higher

colonization rates). Our data thus corroborate the predictions of metapopulation theory that increasing patch isolation will reduce local colonization probabilities; more impermeable landscapes increase the isolation of a site by reducing immigration to it, and thus (re)colonization of empty patches becomes less likely if they are embedded in mostly impermeable matrices. We believe that for community studies such as ours, landscape permeability is a good approximation of patch isolation that permits the modeling of the dynamics of multiple species without the need to account for finer species-specific habitat preferences (such as we did to quantify suitable habitat area). Also, landscape permeability might provide an alternative way to define isolation when distance to the nearest source population (a measure of isolation more relevant to colonization dynamics; Prugh *et al.* 2008) is unknown, because not all habitat patches in the landscape that can potentially sustain a population are sampled.

Landscape permeability was not as good at predicting local extinction as it was at predicting colonization probability. Models including a habitat effect of some kind on extinction probability were usually the top-ranked ones. Moreover, compared with habitat area, the landscape variable scored higher weights less frequently, and in addition to its poorer performance, landscape permeability did not have primarily negative effects on the extinction of species. This may suggest that extinction dynamics in our studied butterfly assemblages are more affected by within-patch habitat features and that permeability of the landscape may be influencing the extinction parameter in two ways simultaneously: both reducing and increasing local extinction risks by, respectively, promoting the arrival of immigrants from surrounding populations (rescue effect) and facilitating emigration when the local habitat deteriorates (Hill, Thomas & Lewis 1996; Kuussaari, Nieminen & Hanski 1996; Mousson, Nève & Baguette 1999).

Compared with the previous factors, topography was not a powerful predictor of extinction dynamics across species, but this covariate reduced extinction risk more often than landscape permeability and performed better at predicting the extinction probabilities of the less mobile species. Indeed, we believe that topography might be buffering extinction in a large number of butterfly species in our study area. However, the importance of this variable becomes strongly apparent only for those species that, because of their low dispersal capacity, are less able to avoid system-wide extinction by colonizing adjacent patches and hence are more sensitive to the local availability of microclimatic refuges. Note that, by virtue of their patchy distribution, such species were underrepresented in our data set compared with the most common and evenly distributed ones. This topographic effect is likely to be more important in cases where a species is close to its southern climatic range boundary (i.e. for the so-called 'rear-edge' populations; Hampe & Petit 2005). The mountainous landscape of our study area could partly account for the seemingly weaker response of

butterfly species to climate warming compared with northern regions. This was already suggested by Parmesan *et al.* (1999) for nonmigratory European butterflies to explain the observed smaller changes in distribution in the southern range. Similarly, in a recent analysis, T. H. Oliver, C. Stefanescu, F. Páramo, T. Brereton & D. B. Roy (unpublished) found a marginal effect of topographic heterogeneity in lowering population variability (and hence extinction risk) in Catalan butterflies, but not in British butterflies, where the landscape is much more homogeneous.

Quite surprisingly, our study indicated a poor predictive power of EP for species extinction and colonization rates, with mostly nonsignificant effects. Local variability in EP thus seemed to contribute very little to the seasonal occupancy dynamics of the butterflies in our study area, despite aridity having been identified as the main predictor of species richness in the Mediterranean basin (Hawkins & Porter 2003; Stefanescu, Carnicer & Peñuelas 2011). There are several reasons that may explain this apparent paradox: coarse grain data (regional climatic data from a 25 km grid matrix may not adequately reflect smaller-scale local climatic conditions), wrong hypothesis (we may have wrongly assumed a central role of EP on larval mortality and adult dispersal or failed to select the most critical periods for some species) and type of state variable (it may be more likely to see effects of climatic variability on abundance than on occupancy parameters). Moreover, in the studies by Hawkins & Porter (2003) and Stefanescu, Carnicer & Peñuelas (2011), mean local aridity condition, rather than interannual variability, was measured. The fact that we could not detect a general effect of our aridity measure on extinction–colonization dynamics may also indicate that deterministic processes (e.g. landscape and habitat change) might have played during our study period a more important role in the persistence of the butterfly species than stochastic processes such as more or less dry years. Local variation in precipitation is one of multiple factors shaping plant assemblages in a site; other factors such as the type of soil, fire regime, grazing and past anthropogenic impacts may influence vegetation composition and structure in a patch. Indeed, all the features that make a patch suitable for a given species are already integrated in our measure of local suitable habitat area, which we have found to be a strong predictor of occupancy dynamics in our butterfly assemblages.

We conclude that increasing environmental quality in the form of increasing suitable habitat area and increasing permeability of the surrounding landscape, together with a more complex topography, all favour species' occupancy in human-altered landscapes and guarantee the coexistence of a large number of species in the studied butterfly assemblages. Conservation planning aimed at maintaining high butterfly diversity should therefore take into account these environmental variables, that is, to manage habitats in and around occupied sites, and to protect sites with

high topographic complexity such as mountain ranges. Moreover, conservation efforts aimed at populations of specialist and less mobile species are also likely to benefit other species in the community.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Life cycle for each butterfly species in our study area.

Appendix S2. Description of the candidate model set and hypotheses underlying the modelling of extinction and colonization parameters.

Appendix S3. Results on summed AIC weights and slope parameter estimates for all species.

Appendix S4. Tables and figures showing species-specific estimates of extinction, colonization and detection probabilities.

Fig. S1. Study area.