

thesis abstract

Assessing the effect of land-cover changes on species distributions: application of habitat models to conservation of Mediterranean bird communities

Sara Vallecillo

PhD, Biodiversity and Landscape Ecology Lab, Centre Tecnològic Forestal de Catalunya, Solsona, Lleida, and Universitat de Lleida, Spain

E-mail: sara.vallecillo.r@gmail.com; <http://biodiversitylandscapeecologylab.blogspot.com/>

Land-cover changes since the last decades of 20th century are leading to important declines in habitat quality, which are responsible for negative impacts on global biodiversity and shifts in species distributions (Steffen et al. 2004). Species distribution models (SDM), which map probabilities of a species' presence based on the correlation between occurrences and several environmental predictors, are thus becoming of prime importance for assessing the response of species to environmental changes (Guisan & Thuiller 2005). SDM-derived maps are also being applied in the selection of priority areas for conservation, an approach that has been encouraged under a global conservation perspective (Rodriguez et al. 2007).

Land-cover changes are geographically variable depending on the ecological and socio-economical context where they occur (Foley et al. 2005). More concretely, in Mediterranean European countries, recent socio-economical transformations have altered traditional agricultural practices and caused the abandonment of less fertile and/or remote rural areas. In these landscapes, the abandonment of human activities leads to shrubland and forest encroachment (Preiss et al. 1997). As a result, fire is becoming the main cause of large-scale habitat disturbance and a major agent in maintaining open habitats and landscape heterogeneity (Lloret et al. 2002). Habitat changes induced by these opposing driving forces (i.e. land abandonment and fire) are expected to be critical in determining future biodiversity patterns (Herrando et al. 2003, Moreira & Russo 2007). This is particularly important for birds, because several open-habitat species have declined alarmingly and many of them have been designated as

species of conservation concern in Europe (BirdLife International 2004). Nevertheless, little is known about how land-cover changes affect patterns of species distribution, and further studies at a landscape scale are needed to assess changes in species occurrence in dynamic landscapes.

Aims and methods

The general aim of my thesis was to identify the ecological processes explaining the distribution of open-habitat bird species in response to the land-cover changes at the landscape scale, emphasizing the role of variations in environmental conditions in space and time. The main processes considered as determinants of land-cover changes in the study area (Catalonia, NE Spain) have been land abandonment and wildfires. In spite of the great impact of fire (130,000 ha of forest burned during the last 20 years of 20th century; Diaz-Delgado et al. 2004), forest extent has not decreased. This is because of the succession that follows land abandonment, leading to forest expansion in abandoned areas. Furthermore, fire has been shown to play a critical role, favouring open-habitat bird species at both local and large spatial scales in the study area (Brotons et al. 2004, 2008).

To evaluate the response of bird species over space and time, SDMs were built using bird occurrence data from the Catalan Breeding Bird Atlas (Estrada et al. 2004) and environmental data (e.g. land use, topography and climate). We first analysed how the role of habitat conditions varied throughout the species' range when building global habitat models. Then we evaluated the capability of habitat models to predict changes over time using bird data from two different time peri-

ods: ca. 1980 and ca. 2000. Finally, SDM-derived maps were applied to select priority areas for conservation of open-habitat bird species. Since conservation decisions ignoring future changes in habitat conditions can fail in promoting species persistence (Pressey et al. 2007), we integrated the potential impact of land-cover changes on conservation areas that are intended to promote the species' persistence in the long term.

Results and discussion

The main results from my PhD thesis derived in four manuscripts, two of them already published. As a first approach to assessing the ecological processes determining changes in species distributions, we evaluated the response curves described by the variation in the occurrence patterns of eight open-habitat bird species along habitat gradients (Vallecillo et al. 2008). We defined a gradient of decreasing farmland proportion for three different landscape settings: a semi-permanent farmland–forest landscape (i.e. with variable proportions of farmland and forests) and two landscape settings that mimic those favoured by land abandonment and fire: a farmland–shrubland landscape and a mosaic landscape (i.e. variable proportions of farmland and forest coexisting with a shrubby matrix). Comparison of the response curves between the different landscape settings allowed analysis of the processes of habitat selection according to variable conditions in the landscape context. In the forest–farmland landscape, we found a dominant negative effect of adjacent forests on species occurrence rates. This overall effect mostly disappeared in farmland–shrubland landscapes composed of two habitats with more similar vegetation structure. In mosaic landscapes, the general negative effect of forests also appeared to be partially compensated by the presence of a shrubby matrix. These results show that habitat loss for open-habitat bird species does not always yield a rapid decline in the occupation rate (i.e. fragmentation process), but rather that each species may show a different response to habitat loss according to the available resources in the landscape context (Brotons et al. 2005a). Landscape gradients induced by fire, and to some de-

gree by land abandonment (both favouring availability of shrublands), may potentially enhance the resilience of threatened open-habitat species at the landscape scale by increasing the range of potential habitats used (Forman 1995, Brotons et al. 2005b).

However, species' responses to environmental conditions may vary geographically as a consequence of the variability in their ecological requirements throughout their ranges (Murphy & Lovett-Doust 2007), thus yielding spatially variable species–environment relationships (Osborne et al. 2007). Using occurrence data for four bird species, we analysed to what extent position within the distribution range, along a gradient of population aggregation, determined geographical variation of distributional constraints (Vallecillo et al. under review). We built generalized linear models for the whole dataset (global models) and separately for different regions within the species' range, according to the decreasing gradient of population aggregation (core, middle and peripheral). For both global and regional models, we compared the species' responses to habitat conditions, showing an overall higher model fit in peripheral regions than in middle and core regions, even after including a spatial factor (i.e. an autocovariate) into these models. The scattered availability of suitable habitat patches in a predominantly hostile landscape matrix seems to be the limiting factor for species distributions in peripheral regions. Conversely, the larger population aggregation in core and middle regions may favour source–sink population dynamics, yielding weaker relationships between habitat conditions and species occurrence (Gimona & Brewer 2006). Geographical variation in distributional constraints can be interpreted as a consequence of the inherent spatial character of ecological processes and their interaction with varying environmental conditions throughout the species range (Fortin & Dale 2005). Overlooking the effects of spatial variation in distributional constraints may lead to erroneous management conclusions and inadequate estimation of the species' response to environmental changes.

The two studies described above showed the important spatial character of the ecological processes determining species distributions at the landscape scale; however, processes are also influenced by the variation in environmental conditions in time. We thus evaluated our ability to predict the effects of land-cover changes on shifts in species distributions at large spatial and temporal scales using Mediterranean landscapes and open-habitat birds as study models (Vallecillo et al. 2009). Based on presence–absence data from the second Catalan Breeding Bird Atlas (1999–2002), we applied six different modelling techniques implemented in BIOMOD (Thuiller 2003) for 10 bird species using climatic, topographic, and land-cover data as predictor variables. Then, we back-projected the models on land-cover conditions from 1980 to evaluate the projections with field-observation data from the first Catalan Breeding Bird Atlas (1975–1983) (Muntaner et al. 1984). Finally, we assessed whether descriptors of fire impact contributed to further explaining species distribution dynamics (i.e. colonization and local extinction), in addition to changes in habitat suitability resulting from land-cover shifts. We developed accurate model projections of current and past global patterns of species distributions, but our ability to predict species distribution dynamics was limited. Colonization dynamics were more strongly related to fire descriptors than to changes in overall habitat suitability derived from land-cover changes. Consideration of ecologically meaningful processes for species (i.e. fire disturbance) when modelling species' distribution might contribute to a better explanation of species' distribution dynamics.

The latter study confirmed the important role of fire regime, for open-habitat bird species, as a key disturbance process driving colonization dynamics in new available habitats. To deal with uncertainties about changes in species' distributions, conservation planning should thus explicitly consider the potential impact of fire on future land-cover changes in the selection of priority areas for conservation. In a fourth manuscript (Vallecillo et al. to be submitted), we selected priority areas for conservation of four groups of bird

species along a general disturbance gradient: forest specialists, forest generalists, mosaic species and open-habitat species. For each group of species, we estimated the vulnerability of the areas with high conservation value to land-cover changes induced by fire. We found that non-forest species (i.e. mosaic and open-habitat species) were positively affected by fire-induced changes, while forest species (i.e. forest specialists and generalists) were negatively affected. Overall, this study emphasizes the need to consider both positive and negative responses of species to fire disturbance. Accounting for the impact of fire on land-cover changes in the selection of areas for conservation reduces the fire risks for forest specialists but increases the risk for non-forest species, in comparison with areas selected before accounting for fire impact. This is especially important for non-forest species, given that we are indirectly conserving the process (i.e. high risk of fire disturbance) favouring the long-term maintenance of their required habitats: open-shrub habitats.

Conclusion

The linkage between the processes of habitat selection (Vallecillo et al. 2008), the geographic variation of environmental constraints (Vallecillo et al. under review) and the distributional dynamics in response to land-cover changes and perturbations (Vallecillo et al. 2009) appears to be fundamental to understanding how the species respond to landscape changes at large spatial scales. This allows development of more adequate recommendations for the species' management and conservation at regional scales (Vallecillo et al. to be submitted). Ignoring the influence of the spatial processes (i.e. interactions between adjacent habitats and their geographic variation) and dynamic processes related to perturbation may result in erroneous conclusions about the species' response to environmental changes and therefore inadequate management and conservation policies. Although this PhD thesis has focused on ecological processes at landscape scale, studies at different spatial scales may improve the understanding of changes in species' distributions. Actu-

ally, it would be advisable to formulate management and conservation policies at different and complementary spatial scales.

Acknowledgements

I would like to thank my supervisor, Dr. Lluís Brotons. I benefited from a FI fellowship with the support from the CUR of the DIUE from the Generalitat de Catalunya and the European Social Fund. This work has received financial support from the Spanish Government project CGL2008-05506-C02-01/BOS.

References

- BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge.
- Brotons, L., Herrando, S. & Martin, J. L. (2004) Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires. *Landscape Ecology*, 19, 663-675.
- Brotons, L., Herrando, S. & Pons, P. (2008) Wildfires and the expansion of threatened farmland birds: the ortolan bunting *Emberiza hortulana* in Mediterranean landscapes. *Journal of Applied Ecology*, 45, 1059-1066.
- Brotons, L., Pons, P. & Herrando, S. (2005a) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *Journal of Biogeography*, 32, 789-798.
- Brotons, L., Wolff, A., Paulus, G. & Martin, J. L. (2005b) Effect of adjacent agricultural habitat on the distribution of passerines in natural grasslands. *Biological Conservation*, 124, 407-414.
- Diaz-Delgado, R., Lloret, F. & Pons, X. (2004) Spatial patterns of fire occurrence in Catalonia, NE, Spain. *Landscape Ecology*, 19, 731-745.
- Estrada, J., Pedrocchi, V., Brotons, L. & Herrando, S. (2004) Atlas dels ocells nidificants de Catalunya (1999-2002). Lynx editor, Barcelona.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. & Snyder, P. K. (2005) Global consequences of land use. *Science*, 309, 570-574.
- Forman, R. T. T. (1995) Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge.
- Fortin, M. J. & Dale, M. (2005) Spatial Analysis: a guide for ecologists. Cambridge University Press, Cambridge.
- Gimona, A. & Brewer, M. J. (2006) Local environmental effects and spatial effects in macroecological studies using mapped abundance classes: the case of rook *Corvus frugilegus* in Scotland. *Journal of Animal Ecology*, 75, 1140-1146.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993-1009.
- Herrando, S., Brotons, L. & Llacuna, S. (2003) Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? *Ibis*, 145, 307-317.
- Steffen, W., Sanderson, A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.J., Turner, B.L. & Wasson, R.J. (2004) Global change and the earth system: a planet under pressure. The Global Change - IGBP Series. Springer-Verlag, Berlin Heidelberg.
- Lloret, F., Calvo, E., Pons, X. & Diaz-Delgado, R. (2002) Wildfires and landscape patterns in the Eastern Iberian peninsula. *Landscape Ecology*, 17, 745-759.
- Moreira, F. & Russo, D. (2007) Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. *Landscape Ecology*, 22, 1461-1476.
- Muntaner, J., Ferrer, X. & Martínez-Vilalta, A. (1984) Atlas dels ocells nidificants de Catalunya i Andorra. Ketres Editor, Barcelona.
- Murphy, H. T. & Lovett-Doust, J. (2007) Accounting for regional niche variation in habitat suitability models. *Oikos*, 116, 99-110.
- Osborne, P. E., Foody, G. M. & Suarez-Seoane, S. (2007) Non-stationarity and local approaches to modelling the distributions of wildlife. *Diversity and Distributions*, 13, 313-323.
- Preiss, E., Martin, J. & Debussche, M. (1997) Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecology*, 12, 51-61.
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M. & Wilson, K. A. (2007) Conservation planning in a changing world. *Trends in Ecology & Evolution*, 22, 583-592.
- Rodríguez, J. P., Brotons, L., Bustamante, J. & Seoane, J. (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions*, 13, 243-251.
- Thuiller, W. (2003) BIOMOD-optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, 9, 1353-1362.
- Vallecillo, S., Brotons, L. & Herrando, S. (2008) Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics. *Biodiversity and Conservation*, 17, 103-119.

Vallecillo, S., Brotons, L. & Osborne, P. E. (under review) Geographical variation in ecological constraints on species distributions along a gradient of population aggregation.

Vallecillo, S., Brotons, L. & Thuiller, W. (2009) Dangers of predicting bird species distributions in response to land-cover changes. *Ecological Applications*, 19, 538–549.

Vallecillo, S., Brotons, L. & Possingham, H. (to be submitted) Minimizing future threats when setting conservation targets for bird species with different response to fire disturbance.

Edited by Núria Roura-Pascual

thesis abstract

On the biogeography of vertebrate body size: ecological and evolutionary insights from assemblage-level patterns

Miguel Ángel Olalla-Tárraga

PhD, Departamento de Ecología, Universidad de Alcalá, Alcalá de Henares, Spain

Current address: Division of Biology, Imperial College London, Silwood Park campus, Ascot, UK.

E-mail: m.olalla@imperial.ac.uk; <http://www.bio.ic.ac.uk/research/apurvis/miguel.htm>

Biogeographers, evolutionary biologists and ecologists have suggested a number of ecogeographical and evolutionary “rules” to describe general trends in the variation of biological attributes across broad spatial and temporal scales. This includes the latitudinal gradient in species richness, as well as Gloger’s, Bergmann’s, Allen’s, Cope’s, Jordan’s, Foster’s and Rapoport’s rules (see Lomolino et al. 2006 or Gaston et al. 2008 for details). Nonetheless, many of these “rules” were originally proposed with insufficient empirical evidence and have reiteratively been called into question. Recent investigations have found exceptions to the proposed patterns and suggested that most of the “rules” are invalid or would need to be reconsidered (see e.g. Ashton 2001).

Under this historical framework, the study of Bergmann’s rule is a paradigmatic example. In 1847, Karl Bergmann suggested that body size plays a major role in determining the geographic distribution of mammals and birds; large-bodied species are favoured in colder climates because of their better heat conservation (lower surface-to-volume ratio). As with the rest of ecological and evolutionary “rules”, both the original pattern and mechanism have not been exempt from criticism. Interestingly, however, after more than 160 years and despite controversies around its validity, Bergmann’s rule still attracts special attention among scientists (Blackburn et al. 1999, Ashton et al. 2000, Meiri & Dayan 2003, Blackburn & Haw-

kins 2004, Rodríguez et al. 2006). This stands in contrast to some other “rules” (e.g. Gloger’s, Allen’s or Jordan’s), whose interest largely remains historic or anecdotic. Such longstanding fascination with Bergmann’s rule is undoubtedly related to the importance of organismal body size in determining physiological, ecological and evolutionary processes.

Along these lines, the debate around the generality of Bergmann’s rule has long been fostered by Ray’s (1960) and Lindsey’s (1966) pioneering observations that some ectothermic organisms also displayed intra- and interspecific body size clines as a response to environmental gradients. Apparently, these findings required alternative explanations to the ones offered for endotherms (Cushman et al. 1993). Since then, researchers have tried to identify ecological or evolutionary mechanisms accounting for geographic body size gradients in ectotherms. A critical step before searching for underlying mechanisms is indeed examining what the patterns look like in nature. Because Bergmann’s rule was originally formulated for endothermic vertebrates, numerous studies have reported the existence of body size gradients in mammals and birds (e.g. Blackburn et al. 1999, Ashton et al. 2000, Meiri & Dayan 2003 and references therein), whereas the geographical variation of body size for many ectothermic organisms remains mostly unknown (but see below).