

## Species–area models to assess biodiversity change in multi-habitat landscapes: The importance of species habitat affinity

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### Abstract

Species–area relationships (SARs) are a common tool to assess the impacts of habitat loss on species diversity. Species–area models that include habitat effects may better describe biodiversity patterns; also the shape of the SAR may be best described by other models than the classical power model. We compared the fit of 24 SAR models, *i.e.* eight basic models using three approaches: (i) single-habitat models, (ii) multi-habitat models which account for the effect of the habitat composition on total species diversity (= choros models) and (iii) multi-habitat models which also account for the differential use of habitats by different species groups (= countryside models). We use plant diversity data from a multi-habitat landscape in NW Portugal. Countryside models had the best fit both when predicting species–area patterns of species groups and of total species richness. Overall, choros models had a better fit than single-habitat models. We also tested the application of multi-habitat models to land-use change scenarios. Estimates of species richness using the choros model only depended on the number of habitats in the landscape. In contrast, for the countryside model, estimates of species richness varied continuously with the relative proportion of the different habitat types in the landscape, and projections suggest that land-use change impacts may be moderated by a species' ability to use multiple habitats in the landscape. We argue that the countryside SAR is a better model to assess the impacts of land-use changes than the single-habitat SAR or the choros model, as species often face habitat change instead of real habitat loss, and species response to change is contingent on their differential use of habitats in the landscape.

### Zusammenfassung

Arten-Areal-Beziehungen sind ein übliches Mittel, um den Einfluss von Habitatverlusten auf die Artenvielfalt abzuschätzen. Arten-Areal-Modelle, die Habitateffekte einschließen, könnten Biodiversitätsmuster besser beschreiben. Auch die Gestalt der Arten-Areal-Beziehung könnte am besten von anderen als dem klassischen Potenz-Modell beschrieben werden. Wir untersuchten vergleichend die Anpassungsgüte von 24 Modellen, genauer 8 Grundmodelle unter drei Ansätzen: 1.) Ein-Habitat-Modelle, 2.) Mehr-Habitat-Modelle, die den Effekt der Habitatzusammensetzung auf die Gesamtartendiversität einbeziehen (= "Choros-Modelle"), und 3.) Mehr-Habitat-Modelle, die auch die unterschiedliche Nutzung von Habitaten durch unterschiedliche Artengruppen berücksichtigen (= "Countryside-Modelle").

Wir nutzten Daten zur Pflanzendiversität für eine Landschaft mit mehreren Habitattypen in NW-Portugal. Die Countryside-Modelle wiesen die beste Anpassung auf bei der Vorhersage von Arten-Areal-Mustern von Artengruppen und der

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Gesamtartenzahl. Insgesamt hatten Choros-Modelle eine bessere Anpassung als Ein-Habitat-Modelle. Wir untersuchten auch die Anwendung von Mehr-Habitat-Modellen auf Szenarien mit sich ändernder Landnutzung. Schätzungen des Artenreichtums mit dem Choros-Modell hingen nur von der Anzahl der Habitate in der Landschaft ab. Dagegen variierten die Schätzungen des Countryside-Modells kontinuierlich mit dem relativen Anteil der verschiedenen Habitattypen in der Landschaft. Projektionen legen nahe, dass die Auswirkungen veränderter Flächennutzung durch die Fähigkeit von Arten, mehrere Habitattypen in der Landschaft zu besiedeln, gemildert werden können.

Wir sind der Meinung, dass die Countryside-Arten-Areal-Beziehung ein besseres Modell für die Abschätzung der Auswirkungen von Landnutzungsänderungen ist als die Ein-Habitat-Arten-Areal-Beziehung oder das Choros-Modell. Der Grund ist, dass Arten oft mit Habitatänderungen anstatt tatsächlichem Habitatverlust konfrontiert sind und die Reaktionen der Arten von ihrer unterschiedlichen Nutzung der Habitate in der Landschaft abhängen.

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## Introduction

Land-use change has been identified as the main driver of biodiversity change and loss in terrestrial systems, not only in the last century but most probably also in this century (MA 2005; Pereira et al. 2010). Direct consequences of land-use change are modification or loss of habitats, which then affect biotic communities and may lead to changes in species richness, species composition and species relative abundance (Pereira, Navarro, & Martins 2012). Species–area relationship (SAR) models have often been used to assess and predict the impacts of habitat loss on biotic communities, namely the extinction of species or populations (Pimm, Russell, Gittleman, & Brooks 1995; Brooks et al. 2002; Malcolm, Liu, Neilson, Hansen, & Hannah 2006; van Vuuren, Sala, & Pereira 2006).

The power model (Arrhenius 1921) is the most commonly used model to describe species–area curves. It defines species richness as a power function,  $S = cA^z$ , where  $S$  is the number of species,  $A$  is the area, and  $c$  and  $z$  are parameters depending, respectively, on the taxonomic group and region under study, and on the sampling regime and sampling scale (Rosenzweig 1995; van Vuuren et al. 2006). However, when studying the effects of land-use change on biodiversity, the power model may fail to capture biodiversity change, due to two inherent limitations. First, it is a single-habitat model, that is, it uses a single variable to describe the size of the area available to species, hence, failing to capture the diversity of habitats, which may be an important descriptor of species richness (Triantis, Mylonas, Weiser, Lika, & Vardinoyannis 2005; Triantis et al. 2008). Second, it also fails to capture the diversity of species responses to land-use changes, which is also an important factor when describing the impact of land use changes on biodiversity. As reported in several studies (e.g., Daily, Ehrlich, & Sánchez-Azofeifa 2001; Barlow et al. 2007; Proença, Pereira, Guilherme, & Vicente 2010), some species are highly sensitive to habitat loss and only occur in native habitats, some species show partial or total tolerance to human-modified habitats, and some species even benefit from the conditions found in human-modified habitats.

Models accounting for habitat heterogeneity (hereafter called multi-habitat models) have been proposed to assess patterns of species richness in multi-habitat landscapes, namely by Tjørve (2002), Triantis, Mylonas, Lika, and Vardinoyannis (2003), and Koh and Ghazoul (2010). These models place a focus on the habitats (habitat diversity, habitat size, species richness per habitat) but not on the response of individual species or groups of species to the different habitats in the landscape. For instance, the choros model defines species richness as a power function,  $S = cK^z$ , where  $K$  is obtained by the multiplication of the number of habitats in an area by the size of that area.

Pereira and Daily (2006) proposed the countryside model. The countryside model builds on the power model and accounts for the existence of different habitats in the landscape and for the differential use of habitats by species. Species are classified in species groups sharing similar habitat affinities, and the estimated species richness of each species group is

$$S_i = c_i \left( \sum_{j=1}^n h_{ij} A_j \right)^{z_i}$$

where  $S_i$  is the number of species in group  $i$ ,  $h_{ij}$  is the affinity of group  $i$  to habitat  $j$ ,  $A_j$  is the area covered by the habitat  $j$ , and  $n$  is the number of habitats. The power model parameters,  $c$  and  $z$ , become species group dependent. The total number of species in the landscape is then given by the sum of species in each group

$$S = \sum_{i=1}^m S_i$$

where  $S$  is the total number of species in the landscape and  $m$  is the number of species groups. The countryside model is particularly suited for biodiversity conservation studies, because it integrates the differential use of natural and human-modified habitats by different species groups, therefore providing more fine-tuned analyses of species responses to habitat change.

Another issue of concern, when using species–area relationships, is to select the model that best describes the shape of the species–area curve. While the power SAR is the model generally used in conservation studies, other functions should be tested as they may describe better the SAR under study (Guilhaumon, Gimenez, Gaston, & Mouillot 2008).

Here we compare the fit of single-habitat models against the fit of multi-habitat models, using diversity data for vascular plants in a multi-habitat landscape. We test eight single-habitat models (power, exponential, negative exponential, monod, rational, logistic, Lomolino, and Weibull; Guilhaumon, Mouillot, & Gimenez 2010) and two multi-habitat models, the choros model (Triantis et al. 2003) and the countryside model (Pereira & Daily 2006), for each of the eight shapes considered for the single habitat models (*i.e.*, 16 multi-habitat models).

We hypothesize that multi-habitat models will perform better than single-habitat models when describing species–area patterns in the landscape because they account for the diversity of habitats in the landscape, and that the countryside model will perform better than the choros model because it also covers the differential use of habitats by species. We also test the use of multi-habitat models as tools to explore scenarios of land-use change.

## Methods

### Study area

This study was conducted in Castro Laboreiro (42° N and 8°10' W; elevation 700–1100 m), a mountain parish in the Peneda-Gerês National Park, NW Portugal (Fig. 1). The first signs of forest loss in this region date back to 5500 BP (Muñoz-Sobrino, Ramil-Rego, & Guitián 2001). Forest loss, probably driven by clearing for grazing and also farming, continued through time and the landscape has been converted into a mosaic of small-scale farms, which are high nature value farmland (EEA 2004), shrublands, and oak forest patches (Honrado 2003). More recently, since the mid-20th century, important social changes have been driving intense rural exodus, leading to farmland abandonment and to the regeneration of natural vegetation cover (Rodrigues 2010). Presently, population density in Castro Laboreiro is low (6.1 people/km<sup>2</sup>, data available at: <http://www.ine.pt>) and agricultural patches are mainly maintained as meadows or pastures. Shrubland is the main type of land-cover (48.1%) in the parish, followed by rock areas with sparse vegetation (32.6%), oak forest (11%) and agricultural land (5.6%) (Rodrigues 2010).

### Sampling design

We selected five 512 m × 512 m habitat mosaics with different land-cover composition: 50% oak forest and 50% shrubland ( $n = 1$ ); 50% oak forest and 50% agriculture ( $n = 1$ ),

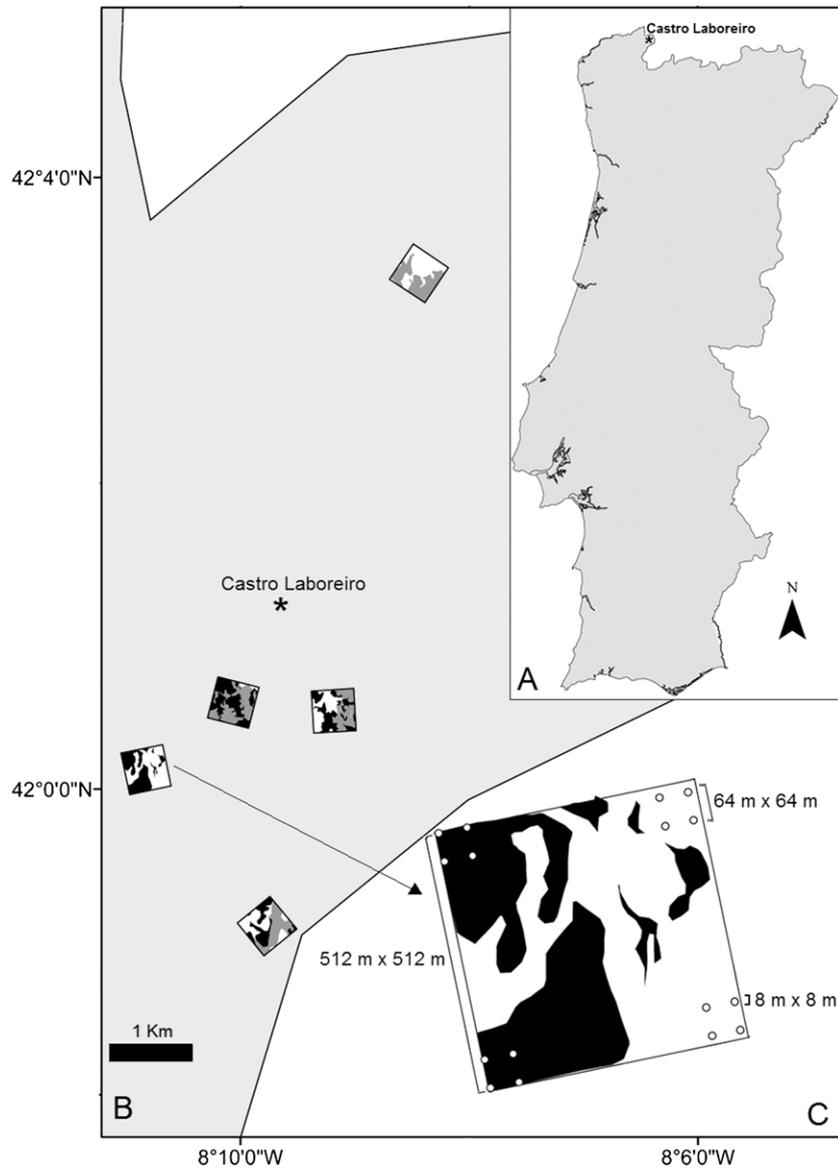
50% shrubland and 50% agriculture ( $n = 1$ ); 33% oak forest, 33% shrubland and 33% agriculture ( $n = 2$ ). We set 64 sampling plots of 1 m<sup>2</sup> (1 m × 1 m) in each mosaic, and recorded presence and percentage cover data of understory plant species (excluding adult trees) using the Braun Blanquet's cover scale (Kent & Coker 1994). The disposition of sampling plots followed a nested design (Fig. 1): 1 m<sup>2</sup> sampling plots were aggregated in groups of four, each plot placed on a corner of a 8 m × 8 m square (64 m<sup>2</sup>), then 8 m × 8 m squares were aggregated in a similar way to form 64 m × 64 m squares (4096 m<sup>2</sup>) and these were finally aggregated in one square (habitat mosaic) measuring 512 m × 512 m (26.2 ha). Most 64 m × 64 m squares were composed of a single habitat type (*e.g.*, forest), the exceptions were two squares composed of forest and agricultural land. Percentage cover of habitat types in each mosaic was calculated using land-cover maps in ArcGIS 9.0 software. Data were collected in June and July 2006.

### Species groups

We performed a principal components analysis (PCA) using species cover data in 1 m<sup>2</sup> sampling plots to sort plant species into groups. Because we used abundance data (measured as percentage cover) and the dataset had many zeros we applied a fourth root transformation to improve normality (Quinn & Keough 2002). Only taxa present in a minimum of five sampling plots were used in the PCA analysis, which totalled 87 species. The remaining taxa were associated with the habitat in which they were observed most frequently (decisions on eventual ties followed the ecologic information in Honrado 2003), and were integrated in one of the species groups defined by the PCA outputs. After the main species groups were formed, we used the Levins index,  $B = 1/\sum x_i^2$ , where  $x_i$  is the relative abundance of the species in the habitat  $i$ , in relation to the species total abundance in the landscape (Levins 1968), to sort ubiquitous taxa ( $B \geq 2$ ).

### SAR models

Species–area patterns in the multi-habitat landscape were determined for each species group separately and for all species. Species–area relationships were fit at the landscape level using species–area data at 1 m<sup>2</sup>, 64 m<sup>2</sup>, 4096 m<sup>2</sup> and 26.2 ha. Fitted curves were similar to a type IIIA curve (*sensu* Scheiner 2003), as we used nested data (1 m<sup>2</sup> to 26.2 ha) from spaced sampling plots, but: (1) we assumed that each scale was well sampled by the 1 m<sup>2</sup> plots (*e.g.*, the 64 m<sup>2</sup> scale was sampled by four 1 m<sup>2</sup> plots at the corners of a 8 m × 8 m square); (2) data were collected from five habitat mosaics of 26.2 ha that were randomly placed in the landscape. Because the sampling scheme follows a nested pattern some spatial autocorrelation should be assumed due to the similarity between species composition in neighbouring plots, but this is an effect inherent to any nested SAR.



**Fig. 1.** Study area location in Peneda-Gerês National Park, NW Portugal (A) and distribution of habitat mosaics in the study area (B). Habitat mosaics are composed of forest (black patches), shrubland (white patches) and agricultural land (grey patches). Nested sampling scheme in a habitat mosaic composed by forest and shrubland (C); see text for more details.

We tested eight single-habitat or base models (power, exponential, negative exponential, monod, rational function, logistic, Lomolino and cumulative Weibull) and two multi-habitat models (countryside and choros model) built on the eight base models, resulting in a total of eight single-habitat models and 16 multi-habitat models (Table 1).

Models were fit in the R environment ([www.cran.r-project.org](http://www.cran.r-project.org)). We used the function *rssoptim* from the *mmSAR* package (Guilhaumon et al. 2010) to fit single-habitat models and the function *nls* from the *stats* package to fit multi-habitat models. Model parameters were fit by least squares, by minimizing the residual sum of squares (RSS). We used the parameter values of the single-habitat models delivered by the *rssoptim* function as starting values for the *nls* function for the multi-habitat models. In case of non-convergence we

altered the values using the values delivered by the trace of iterations delivered by the *nls* function. For initial parameter values of habitat affinity we used 1 for the main habitat of the species group and values three orders of magnitude smaller for the remaining parameters.

Countryside models were simplified before model fitting in order to avoid parameter redundancy and reduce the number of parameters (see Appendix A: Table A1).

Model performance was evaluated using the RSS, the corrected Akaike information criterion,  $AICc = n \log(RSS/n) + 2k(n - k - 1)$ , where  $n$  is the number of data points and  $k$  is the number of parameters in the model, including the estimated variance (the Bayesian information criterion was also applied and delivered similar results), and  $R_{adj}^2$ .

**Table 1.** Formulas and parameters of the eight single-habitat models, and of the multi-habitat models – choros and countryside – built on the single-habitat models.  $S$  is the total number of species,  $S_i$  is the number of species in species group  $i$ ,  $A$  is the area, and  $H$  is the number of habitats;  $c$ ,  $z$ ,  $f$ , and  $h_{ij}$  are model parameters. For the countryside models, only the models to estimate species group richness ( $S_i$ ) are presented, the total number of species is given by  $S = \sum_{j=1}^m S_i$ , where  $m$  is the number of species group;  $h_{ij}$  represents the parameters of habitat affinity (*i.e.*, affinity of species group  $i$  for habitat  $j$ ), for each species group there are as many habitat affinity parameters as habitats. Countryside models were simplified before model fitting, to avoid parameter redundancy and reduce the number of parameters, the simplified models are presented in Appendix A: Table A1.

Model	Formula	Parameters
Single-habitat models		
Power	$S = cA^z$	$c, z$
Exponential	$S = c + z \log A$	$c, z$
Negative exponential	$S = c(1 - e^{-zA})$	$c, z$
Monod	$S = (cA)/(z + A)$	$c, z$
Rational	$S = (c + zA)/(1 + fA)$	$c, z, f$
Logistic	$S = c/(1 + e^{-zA+f})$	$c, z, f$
Lomolino	$S = c/(1 + z^{\log(\beta/A)})$	$c, z, f$
Cumulative Weibull	$S = c(1 - e^{-zA^f})$	$c, z, f$
Choros (K) models		
K.power	$S = c(AH)^z$	$c, z$
K.exponential	$S = c + z \log(AH)$	$c, z$
K.negative exponential	$S = c(1 - e^{-z(AH)})$	$c, z$
K.monod	$S = (c(AH))/(z + (AH))$	$c, z$
K.rational	$S = (c + z(AH))/(1 + f(AH))$	$c, z, f$
K.logistic	$S = c/(1 + e^{-z(AH)+f})$	$c, z, f$
K.Lomolino	$S = c/(1 + z^{\log(\beta/(AH))})$	$c, z, f$
K.Weibull	$S = c(1 - e^{-z(AH)^f})$	$c, z, f$
Countryside (C) models		
C.power	$S_i = c_i \left( \sum_{j=1}^n h_{ij} A_j \right)^{z_i}$	$c, z, h_{ij}$
C.exponential	$S_i = c_i + z_i \log \left( \sum_{j=1}^n h_{ij} A_j \right)$	$c, z, h_{ij}$
C.negative exponential	$S_i = c_i \left( 1 - e^{-z_i \left( \sum_{j=1}^n h_{ij} A_j \right)} \right)$	$c, z, h_{ij}$
C.monod	$S_i = \left( c_i \left( \sum_{j=1}^n h_{ij} A_j \right) \right) / \left( z_i + \left( \sum_{j=1}^n h_{ij} A_j \right) \right)$	$c, z, h_{ij}$
C.rational	$S_i = \left( c_i + z_i \left( \sum_{j=1}^n h_{ij} A_j \right) \right) / \left( 1 + f_i \left( \sum_{j=1}^n h_{ij} A_j \right) \right)$	$c, z, f, h_{ij}$
C.logistic	$S_i = c_i / \left( 1 + e^{-z_i \left( \sum_{j=1}^n h_{ij} A_j \right) + f_i} \right)$	$c, z, f, h_{ij}$
C.Lomolino	$S_i = c_i / \left( 1 + z_i^{\log \left( f_i / \left( \sum_{j=1}^n h_{ij} A_j \right) \right)} \right)$	$c, z, f, h_{ij}$
C.Weibull	$S_i = c_i \left( 1 - e^{-z_i \left( \sum_{j=1}^n h_{ij} A_j \right)^{f_i}} \right)$	$c, z, f, h_{ij}$

Parameter stability across scales and suitability for extrapolation were also inspected. For parameter stability we fitted the models using a reduced data set (1–4096 m<sup>2</sup>) and assessed in pairs the differences between the parameters fitted with the full data set (1 m<sup>2</sup>–26.2 ha) and the parameters fitted with the reduced data set. Differences were calculated as log differences as recommended by Dengler (2009):  $|\log(x_1) - \log(x_2)|$ , where  $x_1$  and  $x_2$  are the pair of parameters fitted with the full and reduced data sets. Differences greater

than 0.3 imply a more than 2-fold difference in parameter values and differences greater than 1 imply a more than 10-fold difference. Suitability for extrapolation was assessed by calculating the log differences between observed species richness in the 26.2 ha habitat mosaics and the richness estimated by the reduced models (extrapolated from the 1–4096 m<sup>2</sup> to a 64-fold larger area).

We also inspected plots of the residuals of the best model (*i.e.*, with the lowest AICc) per model approach to look for

patterns of overprediction or underprediction of species richness.

## Scenarios of land-use change

We used the choros power model, and the countryside power model to estimate total species richness in the landscape in different land-use change scenarios. The power model was selected as the base model for this analysis given its relative good fit to the data, its higher parameter stability and its higher suitability for extrapolation (see Results section).

We used six scenarios: loss of 50% of forest (F50), 50% of shrubland (S50), and 50% of agricultural land (A50), and total loss of forest (F0), shrubland (S0), and agricultural land (A0). In all scenarios we assumed that the area lost by a habitat was replaced by the other two habitats in equal proportions. The current composition of the landscape in the Castro Laboreiro parish (9440 ha) was set as the baseline to calculate land-use changes. For the purpose of these scenarios, we only considered three types of habitat – oak forest, agriculture and shrubland – with all land use transitions occurring among these habitats (*i.e.*, the total area was kept constant and corresponded to the sum of the area currently covered by the three habitat types, 6113.5 ha; the remaining 3326.5 ha are mainly occupied by rock areas with sparse vegetation). Details on land-use transitions in each scenario are presented in Appendix A: Table A2.

## Results

We found a total of 139 plant taxa from 37 families (all identified species were native to the region, see species list in Appendix A: Table A3). Some plants could not be identified at the species level, but we could ascertain that they corresponded to different taxonomic units, so we refer to them as species hereafter.

Three species groups were designated according to the results of the PCA analysis: agricultural species, shrubland species and forest species (see Appendix A: Fig. A1 and Table A3). Taxa were grouped using the value of their loadings on the first and second components of the PCA (both components explained a significant amount of variance under the broken-stick model (Shaw 2003): PC1 – 11.2%, PC2 – 5.4%). PC1 separated agricultural species from forest and shrubland species, and PC2 separated the two latter groups. Ten species were classified as ubiquitous, and were removed from the above species groups to form the ubiquitous species group. In summary, 69 species were classified as agricultural species, 21 as shrubland species, 39 as forest species and 10 as ubiquitous species.

Species responses varied, some species were only observed in a single habitat (*e.g.*, *Melampyrum pratense* in oak forest, *Erica umbellata* in shrubland, or *Lotus pedunculatus* in

agricultural land), while other species were observed in more than one habitat (*e.g.*, *Pteridium aquilinum*, *Agrostis curtisii*, *Hypochoeris radicata*). Overall, we found species from all groups in all surveyed habitats (Table 2). Agricultural habitats were the richest in species (99 species), followed by forest (76 species) and shrubland (53 species).

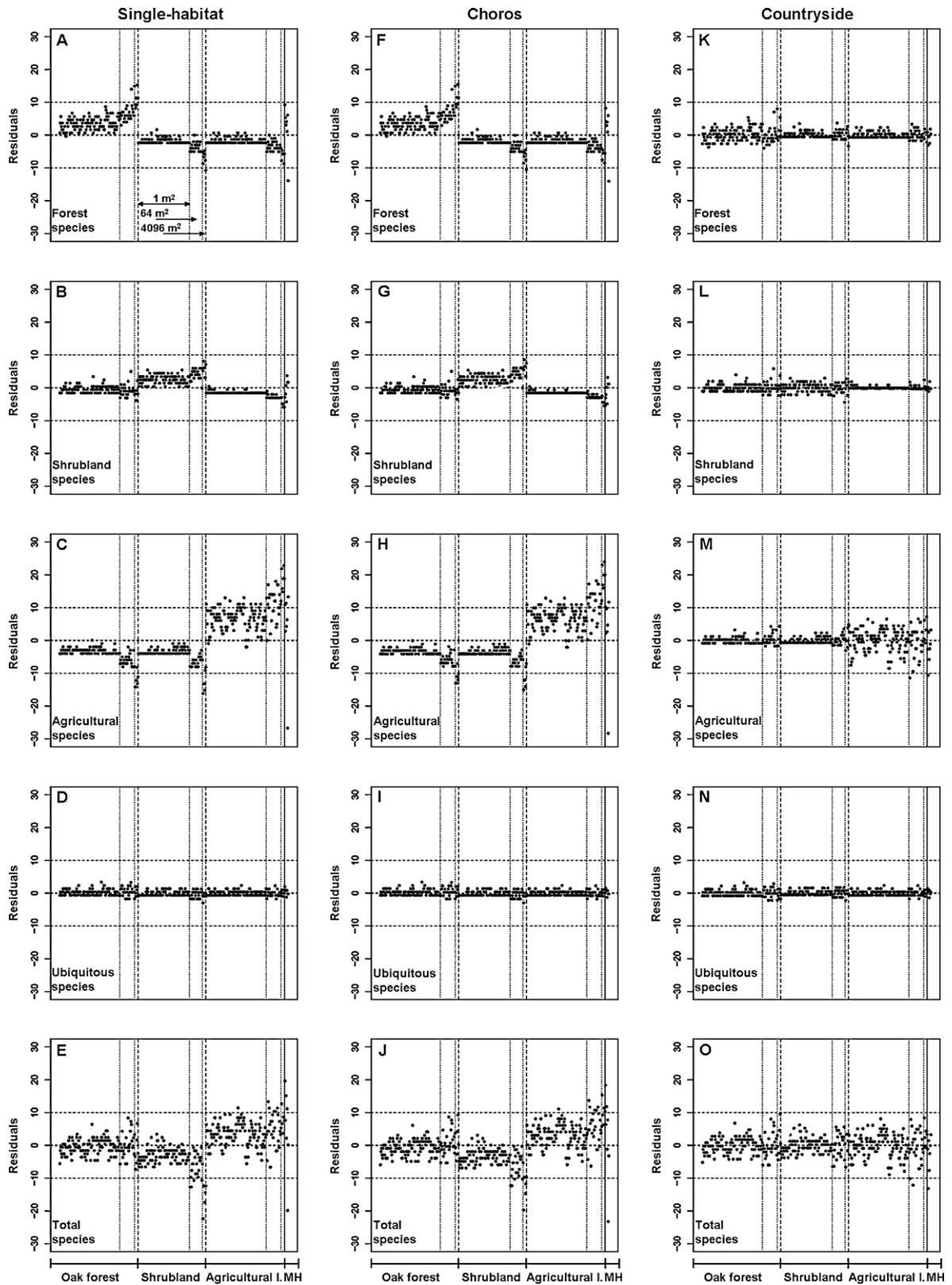
Multi-habitat models had a better fit (*i.e.*, lower RSS and AICc, and higher  $R^2_{adj}$ ) than single-habitat models (Table 3). Choros models had overall a better fit than single-habitat models, with the best choros model performing better than the best single-habitat model (differences in AICc  $\geq 2$ ; Burnham & Anderson 1998) for the forest species, agricultural species, ubiquitous species and total species, and performing as well as the best single-habitat model in the case of shrubland species (difference in AICc = 1).

Countryside models had a better fit than single-habitat models and choros models both when explaining diversity patterns of species groups and of the total number of species (see Appendix A: Table A4). Parameters of habitat affinity indicated a very low affinity of all species groups for alternative habitats ( $h < 0.0001$ ), with the exception of the ubiquitous species.

Among the eight base models, the power model, the Lomolino model and the Weibull model were overall the best fit models. The power model had the best fit in the single-habitat form for all species groups, except the ubiquitous species, and for total species, it also had the best fit for the shrubland, the agricultural species and total species in the choros form. Regarding countryside models, the Lomolino had the best fit for the agricultural, forest and total species, and the Weibull model for shrubland and ubiquitous species (Table 3).

Parameter estimates of the power model (considering single-habitat, choros and countryside models) were stable with mean log differences of 0.02 for the parameter  $c$  and 0.04 for the parameter  $z$  (4% and 9% variation; see Appendix A: Table A5). Parameter estimates of the Lomolino and Weibull models were less stable, with mean log differences above 1 (*i.e.*, more than 10-fold difference) for parameter  $f$  of Lomolino models, and for parameters  $c$  and  $z$  of Weibull models. Extrapolation suitability was similar for the power and Weibull models, with mean log differences between 0.05 and 0.11 (12–28% difference) for the power model and 0.04 and 0.08 (9.6–20% difference) for the Weibull model, and lower for the Lomolino model with a mean log difference of 0.32 (2.1-fold difference) in the case of the single-habitat model (see Appendix A: Tables A6 and A7).

Patterns of plotted residuals also suggest a better fit of the countryside model approach against the choros model and the single-habitat model approaches (Fig. 2). Namely, single-habitat models and choros models tend to underestimate (residuals  $> 1$ ) species group richness in their preferred habitat (*e.g.*, forest species in oak forest) and to overestimate (residuals  $< 1$ ) species group richness in alternative habitats (*e.g.*, forest species in agricultural land). The countryside model does not appear to have such bias, with residuals being



**Fig. 2.** Plots of residuals of the best single-habitat model (left column), the best choros model (central column) and the best countryside model (right column) for forest species (A, F, K), shrubland species (B, G, L), agricultural species (C, H, M), ubiquitous species (D, I, N), and total species (E, J, O). Vertical dotted lines separate spatial scales (1 m<sup>2</sup>, 64 m<sup>2</sup>, 4096 m<sup>2</sup>), vertical dashed lines separate habitats (oak forest, shrubland, agricultural land), and vertical solid lines separate single-habitat data from multi-habitat (MH).

**Table 2.** Number of species (*N* spp.) and number of families (*N* fam.) of each species group observed in each habitat type. The total number of species and families observed by habitat type is indicated in the last row; 51% of forest species (20/39) were unique to forest habitats, 38% of shrublands species (8/21) were unique to shrubland habitats, and 71% of agricultural species (49/69) were unique to agricultural habitats. Shrubland and agricultural habitats shared seven forest species, forest and agricultural habitats shared one shrubland species, and forest and shrubland habitats shared eleven agricultural species.

Habitat type	Forest		Shrubland		Agricultural land		Total spp.
	<i>N</i> spp.	<i>N</i> fam.	<i>N</i> spp.	<i>N</i> fam.	<i>N</i> spp.	<i>N</i> fam.	
Species groups							
Forest species	39	24	10	9	16	10	39
Shrubland species	10	7	21	11	4	3	21
Agricultural species	17	9	14	8	69	23	69
Ubiquitous species	10	9	8	8	10	9	10
Total	76	29	53	22	99	29	

evenly dispersed around zero. Also, the residuals of the countryside model are overall smaller (closer to zero) than the residuals of the other models. Patterns are identical for models of total species (Fig. 2E, J and O), with the residuals of the countryside model being smaller and more evenly distributed around zero.

In land-use change scenarios, projections of species richness varied as a function of land-use changes when using the countryside model and the choros model, however, projections of species richness using the choros model only depended on the numbers of habitats in the landscape (for a fixed area) while projections using the countryside model varied continuously with changes in the proportion of the different habitats (Fig. 3, the detailed values of species richness estimations are presented in Appendix A: Table A2).

In the scenarios F50, S50 and A50, which assumed an intermediate level of habitat loss, the loss of species was moderate (6.9% decrease in forest species, 10% in shrubland species and 8.6% in agricultural species, respectively). In the scenarios F0, S0 and A0, which assumed total habitat loss of one habitat category in each case, the loss of species was greater (26% decrease in forest species, 36.7% in shrubland species and 71% in agricultural species, respectively) but did not imply the total loss of specialist species as it would be expected by applying a single-habitat species–area relationship. Ubiquitous species were less affected by land-use changes and their diversity only decreased in the F0 scenario (9% decrease).

## Discussion

### Evaluation of SAR models

Species–area patterns of plants in our study area were best described by countryside models. In addition, choros models also performed better than single-habitat models. The better fit of the multi-habitat models stresses the relevance of habitat heterogeneity as a descriptor of species richness in multi-habitat landscapes. Furthermore, the better fit of countryside

models, stresses the relevance of also considering species affinity for different habitats and the proportion (size) of each habitat in the landscape. Although more complex than the other SAR models (*i.e.*, with more variables and parameters), the countryside model approach may deliver more accurate accounts of species patterns in multi-habitat landscapes, as it adjusts for the site-specific patterns of selected taxa, being therefore particularly suited to assess the impacts of habitat change on selected species groups. On the other hand, the choros model may be better suited for larger spatial scales that comprise a higher diversity of habitats, and where area and habitat heterogeneity are the dominant processes determining species richness (Triantis *et al.* 2008).

In relation with the shape of the species–area relationship, the power, Lomolino and Weibull models had the best fit to the data. The power model performed better in the single-habitat form and the Lomolino and Weibull models in the countryside form. The better fit of the sigmoidal models suggests that the slope of the SAR may be scale-dependent and associated with patterns of habitat heterogeneity in the landscape. A slower rate of species increase at larger spatial scales, namely at the habitat mosaic scale, is probably explained by the fine-grain of habitat heterogeneity in this landscape leading to a saturation of the species pool at the landscape scale. The need to integrate biological processes on species–area models has been advocated as a way of strengthening the descriptive and predictive power of SARs and their utility for conservation science (Rosenzweig & Ziv 1999; Tjørve 2003). Our results may provide an important contribute towards that end. On the other hand, the existing debate over the shape of SARs (Lomolino 2000, 2002; Williamson, Gaston, & Lonsdale 2001, 2002; Scheiner *et al.* 2011; Triantis, Guilhaumon, & Whittaker 2012) demands further research on the effect of habitat turnover, species affinity, and area on the shape of the SARs.

### Multi-habitat models and species habitat affinity

In many situations and for many species, land-use changes lead to habitat modification and not to a real loss of

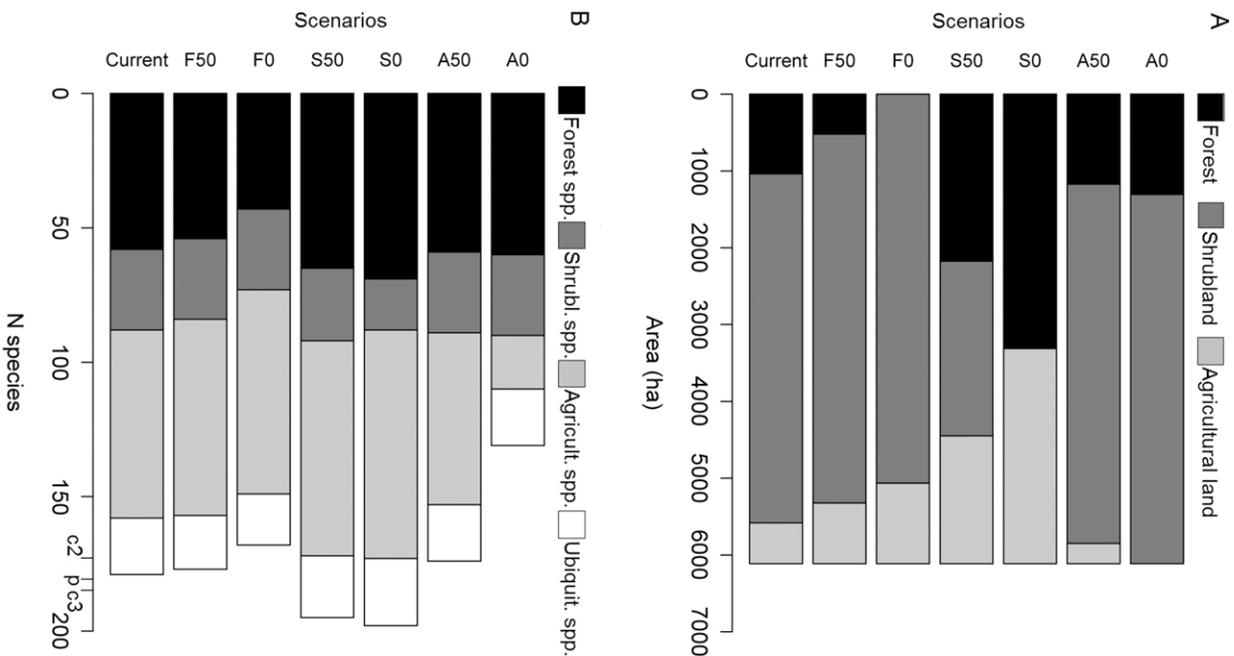
**Table 3.** Species–area relationships of species groups and total species in the multi-habitat landscape. Only the results for the three best fitted single habitat models and multi-habitat models, choros (K) and countryside (C), are presented. Results for all models are presented in Appendix A: Table A4. RSS, AICc, and  $R^2_{adj}$ , provide a measure of models fit to data, with lower values of RSS and AICc, and higher values of  $R^2_{adj}$ , indicating a better fit. Fitted parameters:  $c$ ,  $z$ ,  $f$ ,  $h_F$ ,  $h_S$ ,  $h_A$  ( $h_F$ ,  $h_S$ ,  $h_A$ , are parameters of habitat affinity for oak forest, shrubland, and agricultural land respectively),  $n = 425$  for all SARs. The countryside SARs for total species is expressed by the sum of countryside SARs of species groups.

	$c$	$z$	$f$	$h_F$	$h_S$	$h_A$	RSS	AICc	$R^2_{adj}$
Forest species									
Power	2.3	0.18	–	–	–	–	6366	1156	0.35
Lomolino	$2.3 \times 10^4$	1.20	$7.1 \times 10^{21}$	–	–	–	6366	1158	0.35
Weibull	$2.6 \times 10^4$	$8.92 \times 10^{-5}$	0.2	–	–	–	6366	1158	0.35
K.Weibull	$5.1 \times 10^1$	$4.66 \times 10^{-2}$	0.2	–	–	–	6320	1153	0.36
K.power	2.4	0.17	–	–	–	–	6330	1154	0.36
K.Lomolino	$8.7 \times 10^1$	1.21	$1.2 \times 10^8$	–	–	–	6321	1155	0.36
C.Lomolino	$3.6 \times 10^1$	1.27	$1.4 \times 10^3$	1	$2.3 \times 10^{-7}$	$1.5 \times 10^{-6}$	917	339	0.91
C.Weibull	$2.9 \times 10^1$	0.22	0.21	1	$1.4 \times 10^{-5}$	$4.3 \times 10^{-5}$	919	340	0.91
C.power	6.0	0.14	–	1	$2.3 \times 10^{-7}$	$1.5 \times 10^{-6}$	1084	408	0.89
Shrubland species									
Power	1.6	0.16	–	–	–	–	2452	751	0.25
Weibull	$1.1 \times 10^7$	$1.38 \times 10^{-7}$	0.2	–	–	–	2452	753	0.25
Expo	1.5	0.51	–	–	–	–	2565	770	0.22
K.power	1.6	0.15	–	–	–	–	2448	750	0.25
K.Weibull	$3.8 \times 10^4$	$4.26 \times 10^{-5}$	0.1	–	–	–	2448	752	0.25
K.expo	1.5	0.5	–	–	–	–	2550	767	0.22
C.Weibull	$1.4 \times 10^1$	0.35	$1.9 \times 10^{-1}$	$3.3 \times 10^{-4}$	1	$4.4 \times 10^{-9}$	478	62	0.85
C.power	4.2	0.11	–	$2.1 \times 10^{-5}$	1	$5.8 \times 10^{-14}$	534	107	0.84
C.Lomolino	$1.7 \times 10^1$	1.23	$2.3 \times 10^2$	$3.9 \times 10^{-4}$	1	$1.3 \times 10^{-8}$	917	339	0.72
Agricultural species									
Power	3.9	0.17	–	–	–	–	20,098	1645	0.25
Lomolino	$1.4 \times 10^7$	1.18	$4.2 \times 10^{38}$	–	–	–	20,098	1647	0.25
Weibull	$2.6 \times 10^7$	$1.52 \times 10^{-7}$	0.2	–	–	–	20,098	1647	0.25
K.power	4.0	0.16	–	–	–	–	19,945	1641	0.26
K.Weibull	$8.8 \times 10^4$	$4.55 \times 10^{-5}$	0.2	–	–	–	19,945	1644	0.26
K.logistic	$3.4 \times 10^1$	$3.48 \times 10^{-4}$	1.8	–	–	–	20,723	1660	0.23
C.Lomolino	$6.9 \times 10^1$	1.2	$9.1 \times 10^3$	$4.8 \times 10^{-7}$	$1.9 \times 10^{-7}$	1	2439	754	0.91
C.power	$1.1 \times 10^1$	0.12	–	$3.5 \times 10^{-9}$	$6.9 \times 10^{-10}$	1	2590	778	0.90
C.Weibull	$3.5 \times 10^1$	0.35	0.2	$2.1 \times 10^{-6}$	$1.1 \times 10^{-6}$	1	2731	803	0.90
Ubiquitous species									
Lomolino	$1.2 \times 10^1$	1.30	$5.9 \times 10^4$	–	–	–	344	–82	0.56
Weibull	8.6	0.08	0.2	–	–	–	344	–82	0.56
Power	0.7	0.19	–	–	–	–	353	–72	0.55
K.Lomolino	$1.0 \times 10^1$	1.31	$2.5 \times 10^4$	–	–	–	341	–86	0.57
K.Weibull	7.9	0.09	0.2	–	–	–	341	–86	0.57
K.power	0.8	0.18	–	–	–	–	358	–67	0.55

Table 3 (Continued)

	$c$	$z$	$f$	$h_F$	$h_S$	$h_A$	RSS	AICc	$R^2_{adj}$
C.Weibull	8.2	0.10	$2.6 \times 10^{-1}$	1	0.10	0.37	320	−108	0.59
C.Lomolino	$1.1 \times 10^1$	1.31	$1.3 \times 10^4$	1	0.10	0.37	321	−107	0.59
C.power	0.9	0.19	–	1	0.11	0.42	334	−92	0.58
Total species									
Power	8.6	0.17	–	–	–	–	10,566	1372	0.78
Lomolino	$6.6 \times 10^4$	1.19	$2.3 \times 10^{22}$	–	–	–	10,566	1374	0.78
Weibull	$4.8 \times 10^7$	$1.78 \times 10^{-7}$	0.2	–	–	–	10,566	1374	0.78
K.power	8.8	0.16	–	–	–	–	10,109	1353	0.79
K.Lomolino	$1.1 \times 10^3$	1.18	$2.6 \times 10^{12}$	–	–	–	10,101	1355	0.79
K.Weibull	$5.8 \times 10^2$	$1.5 \times 10^{-2}$	0.17	–	–	–	10,103	1355	0.79
C.Lomolino <sup>a</sup>	$S_{total} = S_{forest} + S_{shrubland} + S_{agricultural} + S_{ubiquitous}$						4294	1027	0.91
C.Weibull <sup>a</sup>	$S_{total} = S_{forest} + S_{shrubland} + S_{agricultural} + S_{ubiquitous}$						4583	1055	0.90
C.power <sup>a</sup>	$S_{total} = S_{forest} + S_{shrubland} + S_{agricultural} + S_{ubiquitous}$						5256	1104	0.89

<sup>a</sup>The parameters of the countryside SARs for total species were fit in groups of four (C.power) or five (C.Lomolino and C.Weibull) per species group (for more details, see Appendix A: Table A1). The values of AICc presented were calculated considering 17 or 21 parameters (number of species groups times the number of parameters of the countryside SARs for each group, plus the estimated variance). These values would probably be lower if the parameters were estimated through a direct fitting of the model.



**Fig. 3.** Scenarios of land-use change: landscape composition (A) and plant richness by species group (B). Predicted values of total species richness in the landscape for each scenario are indicated by the total length of horizontal bars for the countryside power model, and by  $c_2$ ,  $c_3$  and  $p$  in the horizontal axis, for the choros power model ( $c_2$ ,  $c_3$ ) and the power model ( $p$ );  $c_2$  and  $c_3$  are the choros power model predictions for scenarios with two habitats (F0, S0, A0) and three habitats (F50, S50, A50), respectively;  $p$  is the prediction of the power model for all scenarios. See text for a description of scenarios.

inhabitable area, even if habitat quality and therefore species fitness are affected (intense urbanization would be an example of real area loss for many species). Land-use changes are not only affecting communities in natural habitats but are also affecting communities already adapted to human-modified habitats. Specifically, while some regions in the

world, such as tropical regions, are experiencing an intense and fast expansion of agricultural land, in other regions, such as European mountain areas, agricultural land is being abandoned after millennia of human use, leaving space for the regeneration of natural vegetation (Verburg & Overmars 2009; Pereira et al. 2012). Land-use changes in both directions raise concerns about potential effects for biodiversity conservation (Rey Benayas, Martins, Nicolau & Schulz 2007; Acevedo et al. 2010; Leadley et al. 2010). Because some species also use alternative habitats, one should not look just at changes in species patterns in the main habitat (native or other), and assume that all other habitats are inhospitable, since this approach gives an inaccurate assessment of the reality. Therefore, species responses should be assessed at the multi-habitat level.

This can be achieved using the countryside species–area relationship which estimates the habitat affinities of different species groups. We found large differences in the values of affinity for the main habitats and the alternative habitats of each species group, which might be explained by plant communities being a key descriptor of habitats and therefore being closely associated to them (Kent & Coker 1994). Still, showing higher affinity for a habitat does not exclude the use of alternative habitats, even if at much lower abundances. Accordingly, scenario outputs show that several species are expected to persist in the landscape, using alternative habitats, even after the total loss of their main habitat (Fig. 3).

Values of habitat affinity were determined for each species group as a whole. However, the affinity for each habitat varies among species within a group, with some species appearing to be narrow specialists (*i.e.*, observed in a single habitat) and others showing some tolerance for alternative habitats. Moreover, because species groups were based on the current distribution of species in the landscape they should not be perceived as static on a temporal scale. For example, plant species that originally occurred in forest clearings may have flourished with the expansion of open areas for farming, being today more associated with agricultural habitats.

The use of species groups based on the current distribution of species is suitable as a first assessment of species diversity patterns and potential biodiversity changes given scenarios of land-use change. However, a more detailed analysis of species responses to land-use changes requires the use of complementary analyses, such as demographic models (Pereira & Daily 2006). These models could deliver relevant information to better understand species diversity patterns in the landscape, such as the existence of source–sink dynamics. Source–sink dynamics may explain the presence of some species in alternative habitats. That is, individuals observed in an alternative habitat may be migrants from patches of the source habitat, and not be able to thrive in the alternative habitat. In these cases, the persistence of the species in the landscape will depend on the maintenance of the source habitat.

Other authors have proposed models that account for the existence of multiple habitats when studying species–area

patterns. Tjørve (2002) discussed the development of species–area models for multi-habitat landscapes from the combination of the species–area curves of the various habitats in the landscape. Koh and Ghazoul (2010) proposed the matrix calibrated-model, a species–area model also built on the power model, where the  $z$ -value is partitioned in two components: a constant value, equivalent to the observed  $z$ -value in situations where the matrix is totally inhospitable, such as in true islands, and a parameter representing taxa sensitivity to modified habitats. The authors reported a better fit of this model when tested against the power model and the countryside model, on the prediction of extinction risk of endemic birds due to land-use change in 20 biodiversity hotspots. However, although Koh and Ghazoul have used an extensive database of bird species, they did not discriminate species groups and assigned the same values of affinity for human-modified habitats to all species, an approach that does not constitute an adequate testing of the countryside model. The matrix calibrated-model is suited for situations where the original composition of communities is known, or at least where temporal data series exist (*e.g.*, before and after a change in land cover), which precludes its application to systems where present communities result from historical human influence, or where previous data is not available, such as the system discussed in this paper.

## Scenarios of land use change

Two main patterns emerge from the scenario analysis with the countryside model. First, the total loss of a habitat does not imply the total loss of species from the species group more associated with that habitat. While narrow specialists may be more affected, and even become locally extinct, other less specialized species will survive. The proportion of species remaining in the landscape will depend on the level of affinity of the species group to alternative habitats. This explains why agricultural species are more affected by the total loss of agricultural land than forest species by the total loss of forest. This pattern agrees with the theoretical predictions made by Pereira and Daily (2006) on the patterns of biodiversity loss in multi-habitat landscapes. Second, the total richness of species in the landscape is affected by the relative proportion of habitats and by their relative diversity. In our study, total species richness is maximized when the richer habitats (forest and agricultural land) replace the poorer habitat (shrubland). This pattern agrees with the theoretical prediction made by Tjørve (2002) that when habitats have large differences in species diversity, total species richness will be maximized through a higher proportion of richer habitats. Still, land-use changes may also affect other mechanisms controlling plant diversity, such as plant–animal interactions (*e.g.*, pollination), which are not accounted for in these analyses.

In addition, when managing biodiversity at the landscape scale, such as the scale of our study area, it is important to consider diversity patterns at larger scales, namely the regional

scale. In our study area agricultural habitats support a high diversity of species, but these species, being all native, derive from the regional species pool. While extensive agriculture may promote high species richness at the local scale by creating the conditions for the coexistence of many species, it may also cause habitat homogenization (lower species turnover) at larger scales. At regional scales, the spatial turnover of open and closed natural habitats may host as much diversity as extensive farmland, but more research is needed to understand the regional scale patterns (Navarro & Pereira 2012). Also note that while most species may persist in the landscape even after significant land-use changes, large variations may occur in the relative abundance of species, a variable that is not tracked by these scenarios.

## Final remarks

The results presented here support the use of the countryside model approach to assess species–area patterns in multi-habitat landscapes. We recommend that the countryside species–area relationship be used for projections of species extinctions caused by habitat change, replacing the classic approach based on single-habitat species–area relationships.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2012.10.010>.

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