Modelling bird species richness with neural networks for forest landscape management in NE Spain

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Abstract

For preserving biodiversity of European-Mediterranean forest ecosystems in current and future scenarios of global change by means of sustainable forest management it is necessary to determine how environment and forest characteristics correlate with biodiversity. For this purpose, neural networks were used to model forest bird species richness as a function of environment and forest structure and composition at the 1 × 1 km scale in Catalonia (NE Spain). Univariate and multivariate models respectively allowed exploring individual variable response and obtaining a parsimonious (ecologically meaningful) and accurate neural network. Forest area (with a canopy cover above 5%), mean forest canopy cover, mean annual temperature and summer precipitation were the best predictors of forest bird species richness. The resultant multivariate network had a good generalization capacity that failed however in the locations with highest species richness. Additionally, those forests with different degrees of canopy closure that were more mature and presented a more diverse tree species composition were also associated with higher bird species richness. This allowed us to provide management guidelines for forest planning in order to promote avian diversity in this European-Mediterranean region.

Key words: global change; fires; forest biodiversity; forest landscape composition and structure; forest planning; landscape diversity.

Resumen

Modelización de la riqueza de aves mediante redes neuronales para la gestión forestal a escala de paisaje en el NE de España

Para preservar la biodiversidad de los ecosistemas forestales de la Europa mediterránea en escenarios actuales y futuros de cambio global mediante una gestión forestal sostenible es necesario determinar cómo influye el medio ambiente y las propias características de los bosques sobre la biodiversidad que éstos albergan. Con este propósito, se analizó la influencia de diferentes factores ambientales y de estructura y composición del bosque sobre la riqueza de aves forestales a escala 1 × 1 km en Cataluña (NE de España). Se construyeron modelos univariantes y multivariantes de redes neuronales para respectivamente explorar la respuesta individual a las variables y obtener un modelo parsimonioso (ecológicamente interpretable) y preciso. La superficie de bosque (con una fracción de cabida cubierta superior a 5%), la fracción de cabida cubierta media, la temperatura anual y la precipitación estival medias fueron los mejores predictores de la riqueza de aves forestales. La red neuronal multivariante obtenida tuvo una buena capacidad de generalización salvo en las localidades con una mayor riqueza. Además, los bosques con diferentes grados de apertura del dosel arbóreo, más maduros y más diversos en cuanto a su composición de especies arbóreas se asociaron de forma positiva con una mayor riqueza de aves forestales. Finalmente, se proporcionan directrices de gestión para la planificación forestal que permitan promover la diversidad ornítica en esta región de la Europa mediterránea.

Palabras clave: biodiversidad forestal; cambio global; incendios; composición y estructura del paisaje forestal; diversidad del paisaje; planificación forestal.

Introduction

The need for a sustainable forest management that considers not only productive aspects but also the integrity of forest ecosystems and other non-wood values is widely recognized (Lindenmayer *et al.,* 2000; Palahí *et al.,* 2004). Forest management could also play a key role in order to mitigate global change effects. For instance, applying a proactive and adaptive forest management could help to better face climate warming by modifying wildfire behaviour (De Dios *et al.,* 2007). Thus, determining quantitative responses of forest biodiversity to environmental factors occurring in forest systems may be essential for the development of appropriate and well-founded forest management in Mediterranean Europe (Scarascia-Mugnozza *et al.,* 2000). This would additionally help to better understand how forest management can contribute to the mitigation of global change impacts.

The huge growth and development of landscape ecology methods and approaches in the last two decades (Turner, 2005) may significantly contribute to the understanding of the relationships between species and forest beyond the stand scale at which most of the forestry practices are commonly planned. Furthermore, in recent years, the consideration of landscape ecological issues has strongly increased for multi-objective forest planning (*e.g.* Palahí *et al.,* 2004). Valuable biodiversity databases have also been created which can be of great interest for the assessment, management and conservation of forest ecosystems at broader scales than the stand and at the regional level (Fearer *et al.,* 2007).

Ornithological atlas data can be very useful to assess how habitat characteristics are associated with bird distribution at the landscape scale and over large study areas (Donald and Fuller, 1998). Characteristics and processes that determine forest bird distribution may also be influencing other forest living organisms (Donald and Fuller, 1998) since birds play a key functional role in forest ecosystems and are often considered good biodiversity indicators (Sekercioglu, 2006). In this sense, apart from the stand scale, previous studies have shown that forest habitat characteristics are related to bird distribution at different spatial scales (Warren *et al.,* 2005; Yamaura *et al.,* 2005; Mitchell *et al.,* 2006).

With the aim of detecting and modelling complex patterns in applied ecology, such as those likely to occur between environmental factors occurring in forest systems and bird diversity, there has been an increased use of Artificial Neural Networks (ANNs; Thuiller, 2003; Monteil *et al.,* 2004). ANNs have the ability to take into account variables that can be highly correlated with each other or away from the assumptions of normality that presuppose conventional statistical models (Bravo-Oviedo and Kindermann, 2004; Vega-García and Chuvieco, 2006). In this sense, it is noteworthy that ANNs have been widely used for successfully modelling in other forestry fields such as wildfire occurrence prediction (Vega-García *et al.,* 1996; Vega-García and Chuvieco, 2006), hydrology (Alcázar *et al.,* 2008) and wood mechanical properties (García Fernández *et al.,* 2008), among others.

This study aimed at modelling the relationships between forest bird species richness and environmental variables at 1 × 1 km in Catalonia (NE Spain) by means of ANNs in order to provide management guidelines for forest planning and biodiversity conservation in the current and future context of global change. This study also attempts to extend previous models developed by Gil-Tena *et al.* (2007) which (1) mainly focused on the influence of forest landscape characteristics on forest bird species richness, not considering other key environmental variables that may have an increasing relevance in the current changing context and (2) were based on conventional regression techniques that are less powerful as modelling tools and whose predictive capacity is constrained by their parametric assumptions. Considering the robustness of ANNs for detecting complex patterns, we developed a multivariate model assessing the relationship between species richness, forest landscape characteristics, climate, topography and human pressure. Previously, we built univariate networks in order to explore the individual variable response. For ensuring model parsimony in the final multivariate network, we computed several multivariate models following different variable selection strategies; one of them only included the best predictors according to the univariate models. When building the models, simpler network architectures were also preferred in order to obtain ecologically meaningful relationships (see also Monteil *et al.,* 2004) that could be more useful for providing forest management guidelines.

Material and methods

Study area

Catalonia (NE Spain, Fig. 1) is a climatically and topographically heterogeneous region covering 32,107 km^2.
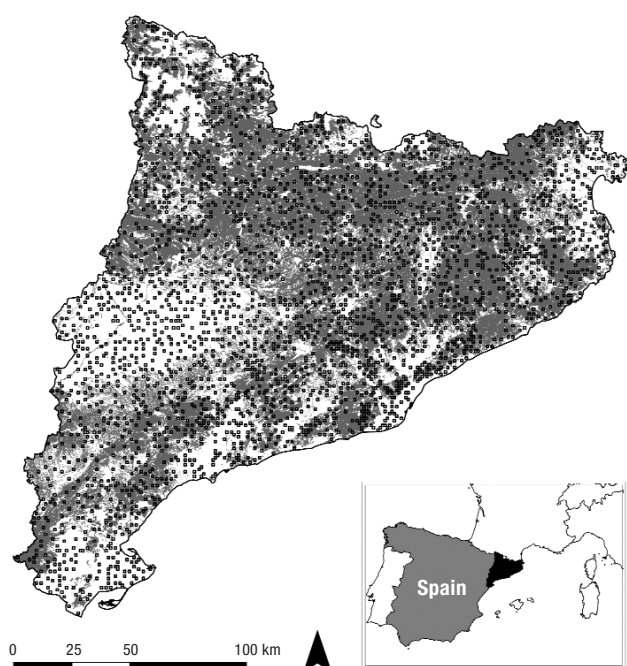
Figure 1. Geographic location of Catalonia (NE Spain), shown in black colour in the lower right chart. The enlarged representation of the study region shows the forest cover (grey colour) and the distribution of the 2,923 1 × 1 km UTM cells (black points) surveyed in the Catalan Breeding Bird Atlas which are here analysed through ANNs.

It includes a variety of habitat types comprising mountainous areas in the Pyrenees (up to 3,143 m) and inland chains, extensive interior and predominantly agricultural plains as the *Plana de Lleida*, and a long coastline along the Mediterranean Sea (with a length of about 300 km). The climate is mainly Mediterranean temperate, with maritime influence in the coast and a cold influence in the Pyrenees. About 38% of Catalonia is covered by forests and approximately 80% of them are privately-owned, with an average ownership size of about 20 ha (Terradas *et al.,* 2004). About one hundred forest tree species are found in this region, although 90% of the total number of trees is from the 14 most common species (mainly of the genera *Pinus* and *Quercus*) (Gracia *et al.,* 2000-2004). The most common forest management practices in the region are those of moderate intensity, such as thinning and selective cutting. In some cases, these practices have increased biodiversity in the understory and canopy of forests, as predicted by the intermediate disturbance hypothesis (Torras and Saura, 2008; Torras *et al.,* 2009). Nevertheless, most forest owners in Catalonia have commonly implemented negative selection cuttings, especially in uneven aged stands. These practices consisted in harvesting the best and biggest trees in the forest, not allowing the stand to reach more advanced development stages (Camprodon, 2001). As a result of the harvesting treatments and the fire occurrence that traditionally affected Catalan forests, the average stand age of most forest typologies is below 50 years (Gracia *et al.,* 2000-2004).

Forest bird data

We estimated forest bird species richness from the census bird data collected by volunteers within the Catalan Breeding Bird Atlas (Estrada *et al.,* 2004) during the period 1999-2002. Forest bird species richness was obtained using presence/absence data of 53 forest bird species from a sample of 3038 1 × 1 km UTM cells (Table 1). Bird species have been considered as forest

Table 1. Forest breeding bird species selected for the analysis

Accipiter gentilis	*Dendrocopos major*	*Oriolus oriolus*	*Serinus citrinella*
Accipiter nisus	*Dendrocopos minor*	*Parus ater*	*Sitta europaea*
Aegithalos caudatus	*Dryocopus martius*	*Parus caeruleus*	*Sylvia atricapilla*
Anthus trivialis	*Emberiza cia*	*Parus cristatus*	*Sylvia borin*
B. buteo	*Emberiza citrinella*	*Parus major*	*Sylvia cantillans*
Carduelis spinus	*Erithacus rubecula*	*Parus palustris*	*Tetrao urogallus*
Certhia brachydactyla	*Falco subbuteo*	*Pernis apivorus*	*T. troglodytes*
Certhia familiaris	*Ficedula hypoleuca*	*Phylloscopus bonelli*	*Turdus merula*
Circaetus gallicus	*Fringilla coelebs*	*Phylloscopus collybita*	*Turdus philomelos*
C. coccothraustes	*Garrulus glandarius*	*Picus viridis*	*Turdus torquatus*
Columba palumbus	*Hieraaetus pennatus*	*Prunella modularis*	*Turdus viscivorus*
Corvus corax	*Loxia curvirostra*	*P. pyrrhula*	
Corvus corone	*Lullula arborea*	*Regulus ignicapilla*	
Cuculus canorus	*M. milvus*	*R. regulus*	

birds on the basis of their differences in the forest and agricultural habitat selectivity indices (see also Gil-Tena *et al.,* 2007) derived from the bird atlas data (Estrada *et al.,* 2004), including some forest species of wide habitat breadth (*e.g. Corvus corone*, *C. corax*, *Embereza cia*, *Picus viridis*). In Catalonia, forest birds are usually associated with advanced development stages (Blondel and Farré, 1988; Suárez-Seoane *et al.,* 2002). Forest bird species' pool does not differ too much from that of the rest of Europe, and few species typical of Catalan forest environments are endemic to the Mediterranean region (Carrascal and Díaz, 2003).

Environmental data

We considered different types of environmental variables, such as those related to forests, topography, climate and human pressure (see the entire list of considered variables in Table 2). These variables can be related to forest bird species richness and thus help to plan forest management for maintaining and enhancing biodiversity and related ecosystem services.

Forest landscape characteristics at the 1 × 1 km scale were obtained from the original vector format of the Spanish Forest Map (SFM) at the scale of 1:50,000 (created within the Third Spanish National Forest Inventory; Ministerio de Medio Ambiente, 1997-2007). From the 3038 UTM cells surveyed in the Atlas, we considered for study 2923 UTM cells that were completely inside Catalonia (Fig. 1), and for which the SFM data were entirely available and updated (excluding the central Catalan areas affected by large wildfires during 1998). The selected forest structure and composition variables at the 1 × 1 km scale were the following:

— Area covered by forests with four different ranges of forest canopy cover (FCC), that is, FCC from 5 to 30% (Forest FCC 5-30%), from 30 to 70% (Forest FCC 30-70%), > 70% (Forest FCC > 70%), and from 5 to 100% (Forest FCC 5-100%).

Table 2. Data sources, summary statistics and units of the variables considered for the modelling. See *Material and methods'* section for abbreviations

Variables		Data source	Mean	Standard deviation	Units
Avian diversity	Bird species richness	ATLAS	12.73	6.51	—
Forest	Forest FCC 5-30%	SFM	6.94	16.88	ha
	Forest FCC 30-70%	SFM	25.27	28.41	ha
	Forest FCC > 70%	SFM	18.24	28.16	ha
	Forest FCC 5-100%	SFM	50.45	36.08	ha
	FCC	SFM	50.54	26.63	%
	Development stage	SFM	2.84	1.29	—
	Coniferous	SFM	47.34	37.69	%
	Development diversity	SFM	0.44	0.33	—
	Tree species diversity	SFM	0.77	0.50	—
	Mono-specific	SFM	12.73	27.36	%
	Burnt area	CDEH	8.45	26.17	ha
Topography	Elevation	SDEM	580	509	m
	Slope	SDEM	12.84	8.21	°
	Aspect diversity	SDEM	1.79	0.29	—
Climate	Annual precipitation	DCAIP	717	208	mm
	Summer precipitation	DCAIP	168	82	mm
	Annual temperature	DCAIP	12.59	3.36	°C
	January temperature	DCAIP	4.92	2.62	°C
	July temperature	DCAIP	21.63	3.64	°C
Human pressure	Protected forest	CDEH	24.23	39.6	%
	Public forest	CDEH	12.67	29.57	%
	Road density	NCGI	0.57	0.72	km/km^2
	Urban area	CDEH	3.00	10.74	%
	Population density	NCGI	268.34	1,295.32	hab/km^2

— Mean forest canopy cover (FCC).

— Mean forest development stage (Development stage), computed as the area-weighted average for each forest patch in the 1 × 1 km UTM cell. We assigned a numerical value for the four different development stages discriminated in the SFM, that is, from recently regenerated to canopy closure (1), from thicket to natural pruning (2), trees with diameter at breast height (DBH)≤20 cm (3) and trees with DBH > 20 cm (4).

— Coniferous species percentage (Coniferous), measured as the percentage of forest land covered by coniferous species.

— Forest diversity variables (the first two quantified through the Shannon-Wiener index):

• Development (Development diversity), obtained from the proportion of forest land area corresponding to the four development stages described above.

• Tree species (Tree species diversity), obtained from the proportion of forest land area covered by each tree species.

• Mono-specific percentage (Mono-specific), measured as the percentage of forest land covered by stands in which at least 90% of the trees correspond to the same (dominant) tree species, as defined for forest management plans in Spain (Madrigal, 1994).

— The accumulated burnt area (Burnt area) in forest fires during the 20-year period before the Atlas survey (1980-2000) was assessed from cartography of fire perimeters gathered by the Catalan Department of Environment and Housing (CDEH; 2007).

Topographic data were derived from the Spanish Digital Elevation Model (SDEM) (Ministerio de Fomento, 1999) and climatic information obtained from the Digital Climatic Atlas of the Iberian Peninsula (DCAIP; Ninyerola *et al.,* 2005) at the spatial resolution of 25 and 200 m, respectively. Topographic variables were mean elevation and slope, and aspect diversity. Climatic variables were mean annual precipitation, mean summer precipitation, mean annual temperature and mean temperature of the coldest and the hottest month (January and July, respectively). Human pressure was assessed by means of considering the percentage of protected forest with regional protection figures and Natura 2000 network, the percentage of public forests managed by the CDEH, the amount of urban areas and population and road density [obtaining the first three variables from the CDEH and the two remaining from the National Center of Geographical Information (NCGI)].

Data analysis

ANNs were built to model the relationships between species richness and independent variables using NeuralWorks Predict® 3.24 software by NeuralWare (2009). A non-linear feed-forward neural network model was used for the estimation of forest bird species richness. The number of layers was set to three (an input, a hidden and an output layer), because this is usually the standard for most problems (Alcázar *et al.,* 2008). Architecture was shaped during training through the cascade-correlation method established by Fahlman and Lebiere (1990). Training was based on an adaptive gradient learning rule (Fahlman and Lebiere, 1990; Bridle, 1990), a variant of the general algorithm of back-propagation (Rumelhart *et al.,* 1986; Werbos, 1994) that had a weight decay factor to reduce complexity of the models (NeuralWare, 2009). This constructive method allowed us to control hidden layer size increments at each step and final network size.

The species richness predictive capacity of each network was evaluated by using the linear correlation (r) between the observed and estimated species richness values in three data subsets (training, validation and test; see below). In the final selection of the best models other diagnostics different from r were also analyzed, such as relative entropy of the network (the lower, the better), internal correlation (the higher, the better) (NeuralWare, 2009), and architecture complexity (we favoured models with lower numbers of input variables, processing elements and layers).

Previously to the construction of the models a 20% of the data was randomly segregated for validation (584 cases). The 80% of the remaining data was also randomly split in two subsets. The first of these subsets contained most of the data (1,637 cases, 70%) and was used for the training process, whereas the smaller subset (702 cases, 30%) was used to periodically test the progression of the learning process and to prevent over-training of the models that might limit their generalization capacity when applied to data not used in the model construction (validation data). By optimizing hidden layer size, the cascade-correlation building technique also contributed to avoid overfitting. Numerous networks were built and trained using different random data samples, training parameters and random initial weights for the connections between nodes. Duplicated networks were run with different combinations of the 2,923 cases randomly split in the three datasets to avoid unfavourable effects due to the selection pro-

cess (*e.g.* getting most of the low-species richness cases in the training data set). Duplicated networks with different random initial weights provided different starting points for the algorithm and rendered the model building process more efficient, avoiding local minimums in the evaluation function.

Since the study also pursued the identification of influential parameters, the determination of significant input variables should be addressed before training. Selection of inputs in this case was based on a genetic algorithm (GA) (Koza, 1993) which evolved a population of variable sets that were selected, mated and mutated for a maximum number of 30 generations in order to find the fittest combination of independent variables for each network model. The GA was selected for its capacity to search through a huge collection of possible solutions, some of which were certain to include interrelated variables. Each variable went previously through a comprehensive number of transformations, which further multiplied the number of possible inputs to the models. Variables should be in an appropriate range for input to the network (–1 to 1), but we also tested several transformations for the continuous numeric independent variables, in order to modify their distribution so that they better matched the distribution of the dependent variable. Then we treated each transformation as an independent variable in the variable selection phase (GA), and as an input to the net in the building process.

The relative rating of influential variables within each network was made through a sensitivity analysis tool provided by NeuralWorks Predict®, which computes a matrix of partial derivatives of the output variable with respect to each of the input variables. The sensitivity analysis produced a quantitative measure of the variation of the forest bird species richness calculated by the network when each Xi variable changed (averaged for all the observations). High values of this sensitivity measure indicated that slight variations of the variable Xi produced considerable changes in the calculated forest bird species richness, and *vice versa*. A positive sign in the sensitivity analysis would indicate a direct relationship between dependent and independent variable; a negative sign would indicate an inverse relationship. This is a standard diagnostic procedure commonly used to gain insight into a multilayer neural network solution (NeuralWare, 2009; Alcázar *et al.,* 2008). Values of frequency selection of each variable in the GA were also assessed. A high selection frequency of a variable in the GA, applied prior to the construction

of each network, was also considered indicative of the importance of that variable in the species richness model. For a more detailed view of ANNs' analysis see Alcázar et al. (2008).

We previously built «univariate» networks (*i.e.* one independent variable that may enter to the network as raw data and/or with different transformations selected by the GA) in order to explore the relationship between species richness and the independent variables and to select the best predictors. For the selection of the best predictors we established a threshold of their *r* values ($r = 0.6$) between the observed and the estimated forest bird species richness for the training data ($n = 1,637$). Afterwards we built multivariate networks with all the set of variables (see Table 2) and with those selected variables that best performed in the univariate networks. Thus, beyond the robustness of the GA procedure, we also wanted to add simplicity to the final model since it may be more parsimonious than without the variable selection.

Results

Forest and climate variables were the variables that attained the best univariate networks in terms of the correlation (*r*) between the observed and the estimated forest bird species richness (Fig. 2). According to these results, the variables selected for the subsequent multivariate network were Forest FCC 5-100%, FCC, July and Annual Temperature, and Summer Precipitation (*r* values for the training data greater than 0.60) (Fig. 2). It is noteworthy that some forest landscape variables, such as Tree species diversity and Development stage, and Elevation performed reasonable univariate networks but their *r* values for the training data were lower than 0.58 (Fig. 2). Nevertheless, the influence on species richness of the amount of forest cover varied according to the different FCC ranges (Fig. 2). Forest FCC 30-70 and > 70% attained the best results (*r* values for the training data of 0.47 and 0.51, respectively), whereas Forest FCC 5-30% poorly modelled forest bird species richness ($r = 0.09$) (Fig. 2). The variables indicating human pressure performed poorly in the univariate networks (Fig. 2). The analysis of sensitivity of the former univariate networks revealed that all the variables obtained positive signs but aspect diversity, temperature, public forest, and road and population density, which showed an inverse relationship (results not shown).
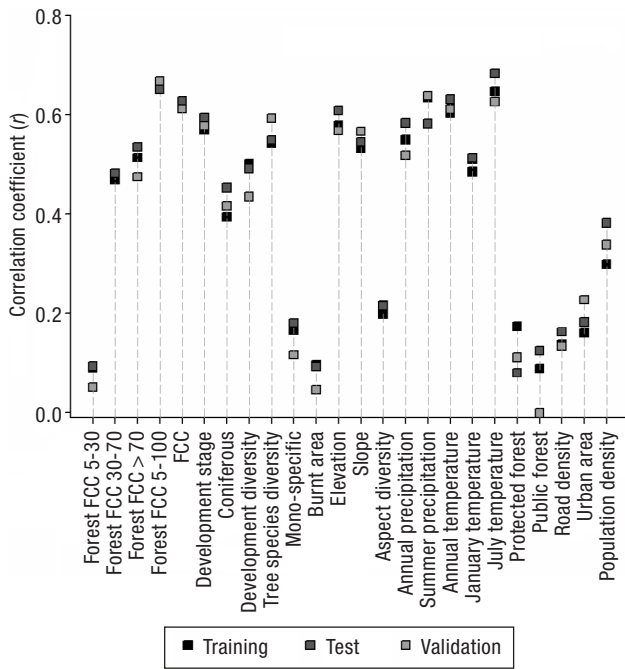
Figure 2. Evaluation of adjustment of the best univariate neural networks assessing forest bird species richness variability by means of the correlation coefficient (*r*) between the observed and estimated species richness.

Figure 3. Sensitivity analysis of the best multivariate neural network assessing forest bird species richness variability. The sign of the average error is shown in brackets.

The best multivariate network had a structure 5-6-1, that is, it had 5 input variables, 6 nodes in the hidden layer, and one in the output layer (species richness) and only included some of the best predictors according to the univariate networks. Other networks that considered all the set of environmental variables presented very complex architectures that prevented their selection as the best multivariate network (results not shown).

In the best multivariate network, the variable Forest FCC 5-100% was incorporated into the model through a log transformation function $\{\log [x/(1-x)]\}$ in the input node, Annual temperature had two entries to the input node (with a linear and a hyperbolic tangent transformation), whereas FCC and Summer Precipitation were incorporated through a linear transformation. According to the sensitivity analysis, Forest FCC 5-100% was the variable presenting a higher influence on species richness, followed by Annual Temperature, Summer Precipitation and FCC in decreasing order (Fig. 3). The selection frequency in the GA roughly agreed with these patterns of variable importance, presenting FCC and Annual temperature a selection frequency of 1 and Forest FCC 5-100% and Summer Precipitation lower selection frequencies (0.93 and 0.87, respectively). July Temperature did not partici-
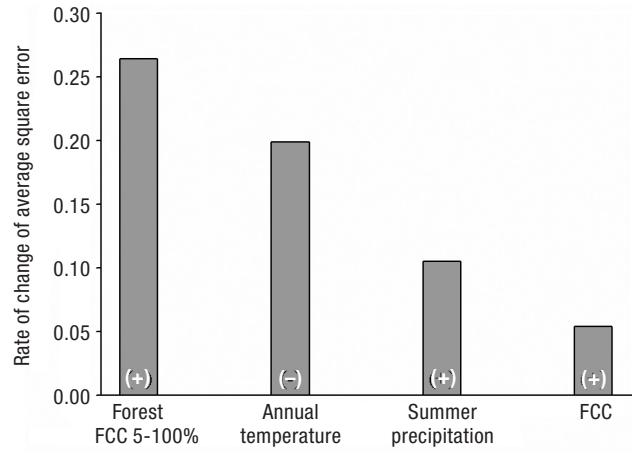
pate in the network construction as anticipated by the comparatively low selection frequency (0.77) in the GA for this variable. The sensitivity analysis also revealed that an increase in Annual Temperature apparently decreased species richness, whereas Forest FCC 5-100%, FCC and Summer Precipitation positively correlated with avian diversity (Fig. 3).

Considering the generality of the analyzed data, which cover an extensive and heterogeneous region (see the description of the study area in *Material and Methods*' section), the multivariate network produced high correlations between the observed and the estimated species richness (*e.g. r* = 0.78 for the training data). Moreover, comparing with the mean of the observed species richness (12.73; Table 2), the mean absolute error was relatively low (3.26 for the training data; Table 3), thus suggesting that this model could be considered a network with a good general behaviour for species richness estimation (*r* = 0.77 for the validation data). Nevertheless, the high maximum absolute error between calculated and estimated species richness in individual 1 × 1 km UTM cells was relatively large (16.72 for the training data; Table 3), indicating a poor

Table 3. Model results for the best multivariate network assessing forest bird species richness variability

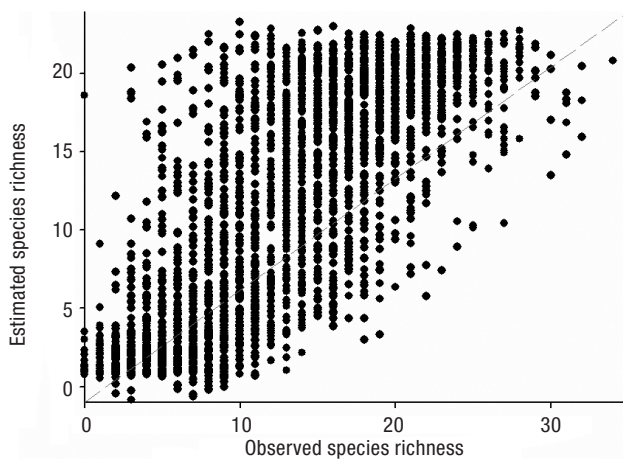|	*r*	Mean absolute error	Maximum absolute error	Records
Training	0.782	3.26	16.72	1,637
Test	0.779	3.29	14.27	702
Validation	0.769	3.47	15.95	584

Figure 4. Graphic evaluation of the multivariate neural network fit.

adjustment in some localized areas, particularly those with the highest species richness (Fig. 4). The other multivariate networks that were discarded because of their complex architectures did not improve the former results in terms of correlations between the observed and the estimated species richness nor the network errors.

Discussion

Forest landscape variables and climate were the best predictors when modelling forest bird species richness in Catalonia. At the scale of our study we assumed that climate may be acting at least partially as a surrogate (González-Taboada *et al.,* 2007) for one or more factors that relate to space and co-vary with climate and are thought to directly influence species richness. On the contrary, forest features are likely to have an effect on breeding bird distribution closer to causality than climate by providing breeding substrates and foraging habitats (Seoane *et al.,* 2004).

According to this general multivariate model, forest bird species richness is positively correlated with the existence of forest with a wide breadth of canopy closure (Forest FCC 5-100%) and negatively associated with high annual temperatures and low summer precipitations. Specific structural characteristics of forest, such as average FCC, also appear to favour species richness but to a lesser extent. On the one hand, the greater influence of forest cover over structural features has also been previously reported by several authors (Westphal *et al.,* 2003; Radford *et al.,* 2005;

Gil-Tena *et al.,* 2007). On the other hand, climate variables may be reflecting other factors limiting forest cover establishment in the region, particularly in those areas with a remarkable Mediterranean climate influence (Thuiller *et al.,* 2003). The type of association between species richness and climate variables agreed with the fact that in Spain most of the forest bird species are more associated with the moistest and most forested northern areas than with the driest southern parts (Carrascal and Díaz, 2003).

The bad performance of the multivariate model at the highest species richness values (Fig. 4) is probably reflecting the need of accounting for the spatial variability of the studied relationships given the extensive area considered ($32,107$ km^2). The broad spectrum of the species richness variable [53 forest breeding bird species of wide habitat breadth (Estrada *et al.,* 2004)] may be also causing difficulties in modelling its variation from a fixed set of predictors. Furthermore, the high species richness could be the result of increased habitat continuity and connectivity with neighboring cells in these locations, which may enhance the species richness and abundance beyond what can be predicted by the environmental and forest variables here analyzed, which do not consider the spatial population processes and connectivity patterns (Gil-Tena *et al.,* 2009a).

Univariate networks were very useful in order to explore the association between the considered variables and species richness, particularly for those predictors that were not included in the final multivariate network. In this case, topography and climate variables (*e.g.* elevation, slope and annual precipitation) also obtained good fits. Nevertheless, there is a lack of direct causal influence of these environmental predictors on species richness as previously stated or a direct link with the measures that can be implemented by forest managers. Therefore, we will focus the discussion on the results of the modelling of species richness as a function of forest landscape and human pressure variables.

More open forests (FCC from 5 to 30%) showed weaker relationships with bird species richness than forests with more closed canopies (FCC > 30%). This result indicated that forests with different proportions of FCC (*i.e.* with a higher FCC diversity) and, particularly, within a particular FCC range seem to be a requirement for higher forest bird species richness. In this sense, Gil-Tena et al. (2007) found that the amount of forest with FCC > 40% attained the best correlation

with total species richness (specialists and generalists) at the landscape scale. Therefore, rather than very open or closed canopies, forest birds seem to prefer stands with a developed overstory and understory (Archaux and Bakkaus, 2007) which could provide more feeding and foraging substrates or nest sites (see Gil-Tena *et al.,* 2007).

Other variables positively but not so strongly associated with forest bird species richness were development stage and tree species diversity. Older forests often harbour more forest bird species (Barbaro *et al.,* 2005; Díaz, 2006; Gil-Tena *et al.,* 2007) by providing more complex structures with more vegetation strata (*e.g.* Venier and Pearce, 2005) or more cavities and a higher amount of dead wood that can be used as breeding and feeding substrates (*e.g.* invertebrates) (Camprodon, 2001). As previously stated, this positive and strong relationship between species richness and development stage could be also explained by the non-Mediterranean biogeographic origin of most of the considered forest birds. Nevertheless, the wide habitat breadth of the considered species may be supporting the positive association between diversity of development stages and species richness (see Gil-Tena *et al.,* 2007).

Forests with a high number of tree species at the landscape scale usually supply greater variety of potentially suitable niches for different bird species than forests with homogeneous characteristics (Hobson and Bayne, 2000; Díaz, 2006; Gil-Tena *et al.,* 2007), as we found in this study. In this sense, the weak association between species richness and the percentage of monospecific stands is supporting the reported favourable effect of tree diversity at scales smaller than 1×1 km. Regarding the type of forest, that is, coniferous or broadleaved species, this seems not to be so determinant for species richness as forest cover or other structural features (see also Mitchell *et al.,* 2006; Gil-Tena *et al.,* 2007). The observed association between coniferous species and forest bird species richness was positive. Nevertheless, as previously shown by Gil-Tena *et al.* (2009b) at this scale (1×1 km) in Catalonia, this relationship is unimodal for both specialist and generalist forest bird species with a maximum at about 50% of total area covered by conifers and 50% by broadleaves, thus indicating the benefit of the coexistence of different types of forest species at the landscape scale. For instance, it is known that broadleaved forests facilitate the establishment of breeding sites, such as in softwood trees (Camprodon, 2001) and

supply a greater availability of arthropods (Illera and Atienza, 1995).

Burnt area in the 20-year period before the Atlas was poorly related to forest bird species richness which agreed with previous studies in Catalonia (Gil-Tena *et al.,* 2009b). The effects of this disturbance have been shown to be more deleterious for specialist than for generalist forest birds (Gil-Tena *et al.,* 2009b) with an apparent increase of edge/generalist species (Ukmar *et al.,* 2007). However, fire has also been shown to be positively associated with several non-forest bird species because of increases in landscape heterogeneity in the Mediterranean (Brotons *et al.,* 2004).

The contradictory relationship between forest bird species richness and urban areas and population density (positively and negatively related to species richness, respectively), could be indicating that, in general, the presence of human settlements do not threaten forest biodiversity unless there is a high population density. Anyway, it seems that the correlation between the presence of human population and biodiversity is scale dependent (Pautasso, 2007) and at coarse scales (c. a grain > 1 km and extent > 10,000 km²) human presence has been shown to present a positive correlation with species richness. Humans tended to settle in areas of high biodiversity (Pautasso, 2007), as in the case of the study area which is located within the Mediterranean basin biodiversity hotspot (Myers *et al.,* 2000). However, long-lasting anthropogenic pressures have profoundly altered Mediterranean forest landscapes and their original biodiversity (Blondel and Aronson, 1999). Our results also showed that the net impact of roads, measured as road density, in forest bird species richness seems to be negative. Road impact, which is understood as more harmful than favourable, differs however according to the considered species (Fahrig and Rytwinski, 2009), with the highly specialized species being usually those most sensitive to roads (Brotons and Herrando, 2001).

Although 80% of public forests are of public utility, prevailing protection objectives over wood production (Terradas *et al.,* 2004), the negative association between forest bird species richness and public forests could be in part explained by the location of these forests in Catalonia, which are concentrated mostly in the Pyrenees. Particularly, in these localities the vegetative period is shorter due to high altitudes, thus limiting forest productivity and associated biodiversity (*e.g.* generalist species). Furthermore, the positive relationship between forest species richness and protected

areas concurs with the fact that reserve planning has been traditionally concentrated on forested areas in the study region. Nevertheless, this type of reserve planning might not be sufficient for the conservation of total biodiversity in Catalonia (Santos *et al.,* 2008) since open habitats and land cover heterogeneity are also required. Moreover, connectivity between these protected areas and the intermediate landscape should be taken into account in the reserve design and territorial planning in this region (*e.g.* Saura and Pascual-Hortal, 2007).

Overall, ANNs allowed us to accurately model forest bird species richness while obtaining a parsimonious multivariate model that was easy to understand. The multivariate network arquitecture indicated that we found a simple and stable model that adequately captured essential relationships in the data. At the same time, this model had a good generalization capability, being able to adequately describe trends in both the model-building (training and test data) and the validation data. Furthermore, ANNs allowed us to model species richness as a function of highly correlated predictors, with r values between explanatory variables up to 0.94 (and particularly for the variables included in the final best multivariate network, $r = 0.57$ between FCC and Forest FCC 5-100% and $r = -0.71$ between Summer Precipitation and Annual Temperature).

Management guidelines for forest planning and concluding remarks

Forest landscape management can enhance forest avian diversity by firstly focusing on forest habitat availability. In addition, to preserve forest bird diversity in Catalonia it would be desirable to promote forest landscapes with different proportions of FCC, a sufficient amount of mature stands and high tree species diversity. Nevertheless, due to the predicted deleterious effects of large and severe wildfires on forest biodiversity in the Mediterranean (Moreira and Russo, 2007), the former concise guidelines should conciliate with the silvicultural treatments focused on fire prevention in order to create forest landscapes less prone to burn that simultaneously allow harbouring Mediterranean forest bird diversity (see also Camprodon and Brotons, 2006). The new forest plans at the district level created by the recent Spanish Forest Law (passed in 2003) could be particularly suitable for integrating these new challenges for managing the forest from a landscape

perspective, aiding to develop successful strategies that ensure the sustainability and integrity of forests ecosystems. For this purpose, and due to the relatively small forest ownership in Catalonia, promoting associationism between forest owners would help to manage and plan at this scale. Furthermore, it is necessary to integrate landscape forest management with other planning strategies and conservation initiatives, such as taking into account the agroforestry mosaics (Santos *et al.,* 2008) or the potential ecological impact of road development (Brotons and Herrando, 2001; Fahrig and Rytwinski, 2009). In addition, managing forest landscape connectivity patterns may be fundamental for species to better face range changes associated with climate change (Opdam and Wascher, 2004).

Adopting a proactive and adaptive forest management could be a guarantee for better facing global change in Catalonia, particularly considering that forest bird species richness was found to be positively related to low temperatures and high precipitations. The fact that in Catalonia 54% and the 29% of the public and private forests, respectively, have a forest plan could be a major starting point for facilitating the transition to these new management and conservation paradigms. These plans are periodically submitted to revision (approximately each 10 years), in which forest management treatments have to be considered together with different types of land use changes. In this sense, regrowth forests in former agricultural lands have been pointed out to be a potential buffer of the impacts of climate change in biodiversity (Bowen *et al.,* 2007). In fact, in the last decades, afforestation and forest maturation seem to have favoured the range expansion of many forest birds in Catalonia (Gil-Tena *et al.,* 2009a) although these dynamics may also be causing an increased fire risk because of landscape homogenization and fuel continuity (Vega-García and Chuvieco, 2006).

To conclude, ANNs have been shown to be useful for describing complex patterns in forest systems. The modelling of forest bird species richness allowed us to reinforce the role of forest management from a landscape perspective in order to develop effective and integrated planning strategies aimed at promoting biodiversity, ensuring the sustainability of forest ecosystem services and mitigating the effects of global changes. These targets are in strong agreement with the positive environmental effects expected from implementing the current Forest Policy Regional Plan of Catalonia (valid for the period 2007-2016).

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