

Biodiversity potential of *Nothofagus* forests in Tierra del Fuego (Argentina): tool proposal for regional conservation planning

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Received: 20 November 2015 / Revised: 11 April 2016 / Accepted: 20 June 2016 /
Published online: 1 July 2016
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Abstract It is difficult to map and quantify biodiversity at landscape level in areas with low data availability, despite demand from decision-makers. We propose a methodology to determine potential biodiversity pattern using habitat suitability maps of the understory plant species with highest cover and occurrence frequency in the three different forests types of Tierra del Fuego (Argentina). We used a database of vascular plants from 535 surveys from which we identified 35 indicative species. We explored more than 50 potential explanatory variables to develop habitat suitability maps of the indicative species, which were combined to develop a map of the potential biodiversity. Correlation among environmental, topographic and forest landscape variables were discussed, as well as the marginality and the specialization of the indicative species. We detected differences in the

Communicated by T. G. Allan Green.

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niches of the species prevailing in the three forest types. The developed map of potential biodiversity uncovered hotspots of biodiversity in the ecotone of *Nothofagus pumilio* and *N. antarctica* as well as in the wettest part of the mixed *N. pumilio*–*N. betuloides* forests. It allowed thus to identify forest areas with different conservation potential and can be readily used as a decision support system for conservation and management strategies at different scales including the identification of land-use conflicts (e.g. of biodiversity with timber production and livestock) and the development of a network of protected areas, which currently does not cover the forests of highest conservation value.

Keywords Ecosystem services · Biodiversity · Habitat suitability · Understory cover · Occurrence frequency · Climatic variables · ENFA

Introduction

Biodiversity conservation offers a paradigm for ecosystem management that incorporates ecological, social, and economic values (Lindenmayer et al. 2012). The role of biodiversity as a regulator of ecosystem processes or as a material output (either a final service or a good), defines the variables of interest when assessing and projecting the impacts of direct drivers. For instance, community data such as species diversity (Mace et al. 2012) may be particularly important to assess the impact of drivers when biodiversity has a regulatory role, while population data, such as species distribution (Gaikwad et al. 2011) would be more adequate when biodiversity elements have a direct use value. Beyond the obvious benefits to the natural environment, biodiversity also provides other quantifiable services. For example, biodiversity annually provides trillions of US dollars for ecosystem processes and services provision (Costanza et al. 1997) influencing over the most recognized functions: provisioning, regulating and cultural (MEA 2005). For this reason, it is necessary to quantify the impacts of different management and conservation alternatives on biodiversity (Lindenmayer et al. 2012) and to understand the trade-offs and synergies associations between the different management and conservation proposals (e.g. Nelson et al. 2009; McShane et al. 2011).

There are many studies that map biodiversity at global and regional scale in areas with large quantity of reliable long-term data (Bowker 2000; Ferrier 2002; Naidoo et al. 2008). However, there are large regions with poor data availability (e.g. see some gap areas in the database of The Global Biodiversity Information Facility, Yesson et al. 2007). In this context, there is a need to develop new spatially explicit methods to map and quantify the biodiversity potential and the spatial associations with landscape factors at regional scale. In recent decades, different methods have been increasingly applied to estimate the geographic extent of the fundamental ecological niche for different organisms, based mostly in coarse-scale climate dimensions (Estrada-Peña and Venzal 2007). The extent of the ecological niche can be estimated through: (i) a mechanistic approach (Guisan and Zimmermann 2000) or physical modelling, where responses of species to explanatory variables are determined by direct measurement, or (ii) by a correlative approach that relates species occurrence to explanatory variables associated to this occurrence (Hirzel et al. 2002). In the framework of this last approach, species distribution modelling links species records with a set of variables, building a mathematical function that can be interpolated or extrapolated to areas with a lack of information on the focus species (Guisan and Zimmermann 2000),

e.g. developing habitat suitability maps (HSM) for some specific species. These techniques are being increasingly used in solving a variety of problems, including environmental requirement of the species, adaptations of species or climate change impact over species assemblage (Bourg et al. 2005; Peterson 2006; Jiménez-Valverde et al. 2008; Dullinger et al. 2012). One of the most innovative uses is related to biodiversity conservation including highlight areas for endangered species translocations and to design new natural reserves focused on single (Peterson 2006) or multiple species (Poirazidis et al. 2011).

In Argentina, a recent national legislation (National Law 26331/07) regulates the uses and management of native forest lands, promoting the conservation in both, private and state lands. However, the criteria followed to define the management strategies did not consider biodiversity values (e.g. target species to protect, or distribution of more susceptible species) and are not included in the environmental and forest management decision making processes. Because the lack of reliable data or tools to identify areas with special conservation values, most conservation efforts had been dedicated to marginal unproductive forests. This problem could be overcome by the development of mapping tools on biodiversity distribution that allow policy makers to develop better strategies based on indicator species. Vascular plants are important descriptors of physical environmental variables such as climate, topography and soils (Landsberg and Crowley 2004) and understory plants have been used to describe the environmental impact of human activities such as forestry (Lencinas et al. 2008, 2011) or cattle grazing (Peri et al. 2013). For this, the use of vegetation mapping can be useful as primary tool for defining conservation priorities at regional level.

At the austral extreme of South America, Tierra del Fuego Island hosts the world's southernmost forested ecosystems, located in one of the least disturbed eco-regions on the planet (Mittermeier et al. 2003). However, there is a significant gap in our knowledge about the distribution of plants species linked to regional environmental variables. The main objective of this study was to elaborate a decision tool based on a map of potential biodiversity (MPB) using habitat suitability maps for the understory plant species with highest cover and occurrence frequency in different forests types of Tierra del Fuego (Argentina). By relating climate and topographic variables with the potential biodiversity values, we additionally aim at defining environmental thresholds for the different forest types on the study area. We propose to use the MPB for conservation strategies development, and compare detected biodiversity hotspots with the conservation strategy promoted by the National and Provincial Governments for the region.

Methods

The study was carried out for Tierra del Fuego province (Argentina) (52°40' to 55°03'S, 65°06' to 68°36'W), which covers 21,300 km². Here, the Andean Mountains run from W to E and define the relief and climate pattern of the region, which is under strong influence of the vicinity of Antarctica. A rainfall gradient from North (dry) to South (wet) defines the vegetation types in Tierra del Fuego, with grasslands in the north and forests in the south. This province has a population density of 6.0 inhabitants km⁻² mainly located in two cities (97.5 % of the total population), close to ranching and oil extraction areas and close to major tourism areas, respectively. National parks and provincial reserves mainly preserve landscapes of high aesthetic or heritage value, where forests are included as long as they are not important for timber interests (Fig. 1) (Martínez Pastur et al. 2015).

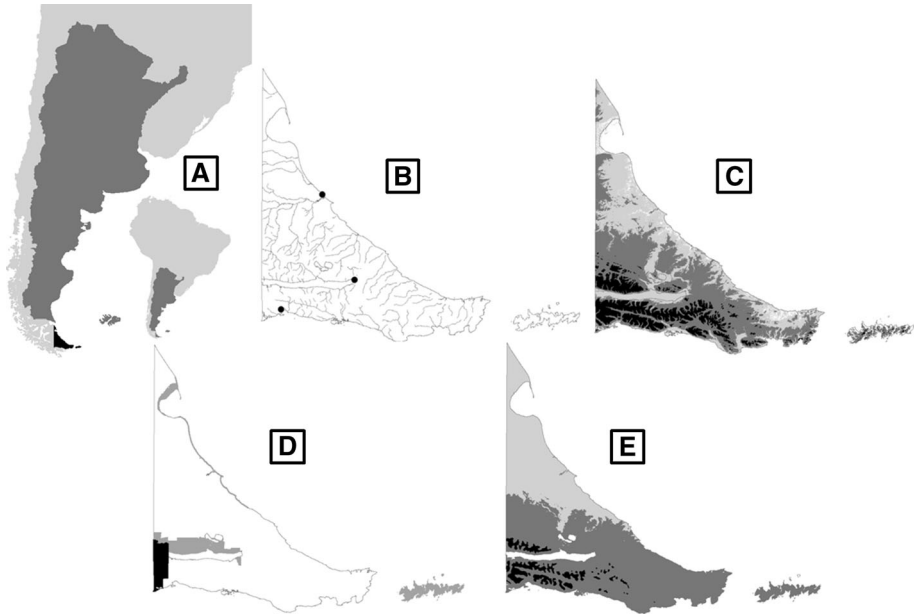


Fig. 1 Characterization of Tierra del Fuego (Argentina): **a** location (*black* = Tierra del Fuego); **b** cities (*black dots*) and main water bodies (coast, lakes, lagoons and rivers); **c** relief (*grey* = 0–100 m.a.s.l., *dark grey* = 100–400 m.a.s.l., *black* = >400 m.a.s.l.); **d** protection areas (*grey* = provincial reserves, *black* = national parks); and **e** vegetation types (*grey* = grassland and shrub-land steppe, *dark grey* = *Nothofagus* forests, *black* = alpine vegetation) (modified from Martínez Pastur et al. 2015)

We elaborated a map of the potential biodiversity (MPB) for the forest areas in Tierra del Fuego (Fig. 2). First, we classified the forests into three broadleaved forest types based on Moore (1983): (i) deciduous *Nothofagus antarctica* forests, (ii) deciduous *N. pumilio* forests, and (iii) mixed forests of deciduous *N. pumilio* and evergreen *N. betuloides* forests. Shapes of the cover area of these forest types were obtained from the provincial forest inventory (Collado 2001), and were rasterized at 90×90 m resolution using software ArcView 3.0 (ESRI 1996).

Second, we used a database of vascular plants based on a survey of 535 plots sampled between 2000 and 2012 as part of a regional monitoring network in ecology and biodiversity (PEBANPA, Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral) in which several federal institutions are involved (UNPA, INTA, CONICET). This database included data on plant species cover (%) and occurrence frequency (%) in the understory (D'Amato et al. 2009). A total of 35 vascular plant species indicators were selected by choosing the 20 most important species (cover \times frequency of occurrence) for each of the three forest types (Table 1).

Third, we explored more than 50 potential explanatory variables for the modelling. A Pearson's correlation analyses was conducted (see Table 4), and 15 variables were finally selected for the modelling based on the lowest values of correlation indices obtained when paired analyses were conducted among them. This selection included seven variables related to climate, two related to topography and six to forested landscape metrics (Table 2). The climate variables were related to temperature (annual, max of warmest month or min of coldest month), rainfall (annual or warmest quarter) or both (global

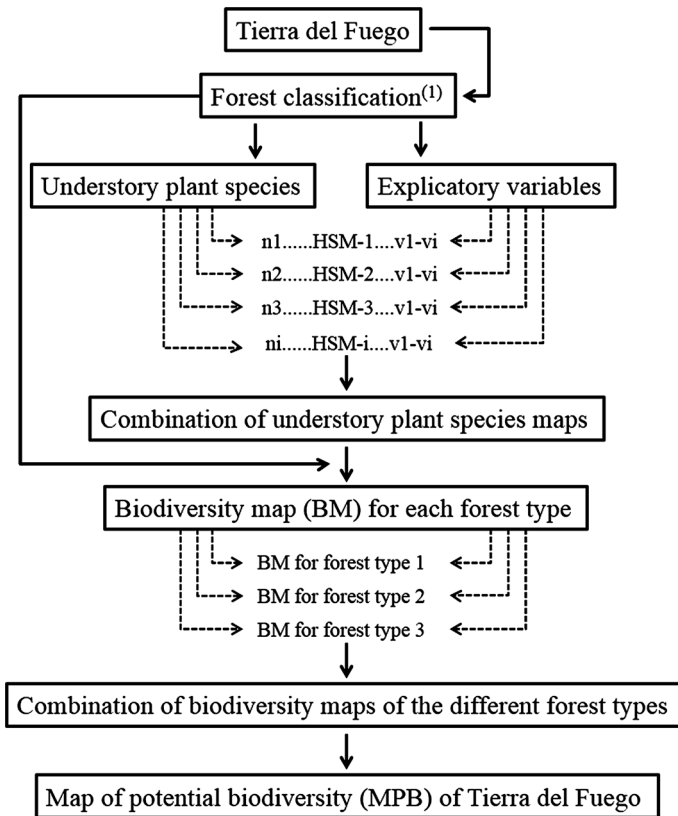


Fig. 2 Chart flow of the methodology and map construction, (1) Based on Collado (2001)

potential evapo-transpiration and global aridity index) (Hijmans et al. 2005; Zomer et al. 2008). The topography variables were defined by the altitude and the slope (Farr et al. 2007). Finally, the forest landscape metrics (Collado 2001) derived from Fragstats software (McGarigal et al. 2012) were associated to edge density, largest patch index and proportion of total forests of the different forest types.

Using Ecological Niche Factor Analysis (ENFA, Hirzel et al. 2002) we performed a series of spatially explicit habitat suitability models for the 35 vascular plants in the Biomapper 4.0 software (Hirzel et al. 2004a). The ENFA modelling technique computes a group of uncorrelated factors with ecological meaning, summarizing the main environmental gradients in the considered region (Chefaoui and Lobo 2008). ENFA calculates a measure of habitat suitability based on an analysis of marginality (how the species' mean differs from the mean of all sites in the study area) and environmental tolerance (how the species' variance compares with the global variance of all sites) or specialization (tolerance⁻¹). Models of the understory plants were generated from the species-presence data in the 535 surveys and the fifteen selected environmental explanatory variables.

The resulting habitat suitability maps (HSM) had scores that varied from 0 (minimum habitat suitability) to 100 (maximum). The explanatory variables were normalized through a Box-Cox transformation (Sokal and Rohlf 1981), and a distance geometric-mean algorithm, which provides a good generalization of the niche (Hirzel and Arlettaz 2003), was

Table 1 Species group (DICO = dicots, MONO = monocots, PTERI = pteridophyta), scientific name and code, presenting the mean cover (%) and the frequency of occurrence (%) between brackets, followed by the rank (1–20) for the 20 most important species of the three studied forest types (NP = *Nothofagus pumilio* forests, NA = *N. antarctica* forests, MIX = mixed forests)

Group	Species	Code	NA	NP	MIX
DICO	<i>Acaena magellanica</i>	ACMA	0.72(52)14	0.49(24)17	–
DICO	<i>Acaena ovalifolia</i>	ACOV	1.31(47)13	0.63(25)12	–
DICO	<i>Adenocaulon chilense</i>	ADCH	–	0.53(21)20	0.28(12)19
DICO	<i>Berberis buxifolia</i>	BEBU	1.19(70)08	0.52(23)18	0.51(18)15
PTERI	<i>Blechnum penna-marina</i>	BLPE	4.68(52)04	0.90(19)13	1.15(26)06
MONO	<i>Bromus unioloides</i>	BRUN	1.28(41)15	–	–
DICO	<i>Cardamine glacialis</i>	CAGL	0.69(61)11	0.23(41)09	0.06(12)20
DICO	<i>Cerastium arvense</i>	CEAR	0.53(47)16	–	–
DICO	<i>Chilotrichum diffusum</i>	CHDI	–	–	0.80(12)17
MONO	<i>Codonorchis lessonii</i>	COLE	–	–	0.62(42)04
DICO	<i>Cotula scariosa</i>	COSC	6.32(77)01	–	–
MONO	<i>Deschampsia flexuosa</i>	DEFL	2.02(45)12	–	–
DICO	<i>Dysopsis glechomoides</i>	DYGL	–	1.65(41)04	0.31(14)18
DICO	<i>Empetrum rubrum</i>	EMRU	–	0.77(20)16	1.46(20)08
MONO	<i>Festuca magellanica</i>	FEMA	2.63(65)06	1.15(48)05	–
DICO	<i>Galium aparine</i>	GAAP	3.08(82)03	2.24(37)03	–
DICO	<i>Galium fuegianum</i>	GAFU	0.44(41)18	–	–
DICO	<i>Gunnera magellanica</i>	GUMA	–	2.23(29)06	0.53(18)14
PTERI	<i>Hymenophyllum secundum</i>	HYSE	–	–	1.09(18)11
MONO	<i>Luzuriaga marginata</i>	LUMA	–	–	0.46(20)12
DICO	<i>Macrachaenium gracile</i>	MAGR	–	–	0.25(30)07
DICO	<i>Osmorhiza chilensis</i>	OSCH	3.79(38)09	2.98(25)02	1.21(18)10
DICO	<i>Osmorhiza depauperata</i>	OSDE	5.01(76)02	3.31(45)01	0.70(18)13
DICO	<i>Pernettya mucronata</i>	PEMU	–	0.93(18)14	1.84(42)03
DICO	<i>Pernettya pumila</i>	PEPU	–	–	2.53(42)02
MONO	<i>Phleum alpinum</i>	PHAL	1.77(59)10	0.64(26)11	–
DICO	<i>Ribes magellanicum</i>	RIMA	–	–	0.38(18)16
DICO	<i>Rubus geoides</i>	RUGE	–	1.02(36)08	2.01(58)01
DICO	<i>Schizeilema ranunculus</i>	SCRA	2.28(64)07	–	–
DICO	<i>Senecio acanthifolius</i>	SEAC	–	1.52(38)07	0.61(34)05
DICO	<i>Taraxacum gillesii</i>	TAGI	0.60(36)19	–	–
MONO	<i>Trisetum spicatum</i>	TRSP	3.46(62)05	0.25(28)15	–
MONO	<i>Uncinia lechleriana</i>	UNLE	0.89(39)17	0.55(21)19	–
DICO	<i>Vicia magellanica</i>	VIMA	0.33(27)20	–	–
DICO	<i>Viola magellanica</i>	VOMA	–	0.95(25)10	0.85(24)09

chosen to perform the analyses. All continuous independent variables were referenced to the same 90 × 90 m grid squares as the species data. Each HSM map was evaluated by a cross-validation process (Boyce et al. 2002, and further developed in Hirzel et al. 2006), using the Boyce index (B), the proportion of validation points (P) and the continuous Boyce index (Bcont). Also, we used the absolute validation index (AVI, defined as the

Table 2 Explanatory variables used in modelling habitat potential for understory plant species (NP = *Nothofagus pumilio* forests, NA = *N. antarctica* forests, MIX = mixed forests)

Category	Description	Code	Unit	Data source
Climate	Annual mean temperature	AMT	°C	WorldClim ^a
	Max temperature of warmest month	MAXWM	°C	WorldClim ^a
	Min temperature of coldest month	MINCM	°C	WorldClim ^a
	Annual precipitation	AP	mm year ⁻¹	WorldClim ^a
	Precipitation of warmest quarter	PWQ	mm year ⁻¹	WorldClim ^a
	Global potential evapotranspiration	EVTP	mm year ⁻¹	Consortium for spatial information ^b
	Global aridity index	GAI		Consortium for spatial information ^b
Topography	Altitude	ALT	m.a.s.l.	DEM ^c
	Slope	SLO	%	DEM ^c
Landscape	Forest edge density	ED	m ha ⁻¹	Map of forest types ^d /Fragstats ^e
	Forest largest patch index	LPI	ha	Map of forest types ^d /Fragstats ^e
	Proportion of NA forests	PL_NA	%	Map of forest types ^d /Fragstats ^e
	Proportion of NP forests	PL_NP	%	Map of forest types ^d /Fragstats ^e
	Proportion of MIX forests	PL_MF	%	Map of forest types ^d /Fragstats ^e
	Proportion of forests	PLAND	%	Map of forest types ^d /Fragstats ^e

^a Hijmans et al. (2005)

^b Zomer et al. (2008)

^c Farr et al. (2007)

^d Forest types are based on Collado (2001)

^e McGarigal et al. (2012)

proportion of validation cells with habitat suitability >50), and the contrast validation index (CVI, defined as $AVI - AVI > 50$ and indicating thus how much the model differs from a random model of habitat suitability) (Hirzel and Arlettaz 2003). After this stage, we combined for each forest type the HSM of the 20 most important understory plant species (Table 1) to generate one biodiversity map (BM) for each forest type using ArcView 3.0 (ESRI 1996) (Fig. 2). These created maps show in each pixel the average HSM values of the 20 understory plant species, as an indicator of potential biodiversity of the site (0 minimum and 100 maximum potential biodiversity). Finally, we combined the three BM forest types into one single map (MPB) for the entire Argentinian part of Tierra del Fuego Island. Finally, grids from BM of each forest type, and climate and topographic variables were related to each other in ArcView 3.0 (ESRI 1996) to analyse the environmental thresholds for the different forest types and range values of the potential biodiversity. For this purpose we calculated for all three forest types for each environmental predictor mean and standard deviation of the low, middle and high third values of pixels. The limits were set so that the three classes contained an identical quantity of pixels.

Results

The 35 understory plant species that included the 20 most important species of each of the three forest types in Tierra del Fuego included 2 ferns, 8 monocots and 25 dicots (Table 1). Eight species (2 monocots and 6 dicots) were exclusive for *Nothofagus antarctica* forests of the northern part of the study area, seven species (1 fern, 2 monocots and 4 dicots) were exclusive for the mixed forests in the south, whereas not any species was exclusive for the *N. pumilio* forests in the central part of the Island. However, *N. antarctica* and *N. pumilio* forests shared seven species of the dataset, *N. pumilio* and mixed forests shared eight species, while five species were shared by all three forest types. The selected species did not present higher covers into the forests (a gradient of 0.06 % for *Cardamine glacialis* in the mixed forests to 6.32 % for *Cotula scariosa* in *N. antarctica* forests), but most of those had greater frequencies of occurrence across the landscape (12 % to 82 %) influencing over the understory species assemblage of the different forest type.

The HSMs obtained from the 35 plant species showed good validation statistics, where the explained information varied from 70 to 99 % (Table 5). *Nothofagus antarctica* forests presented comparably high values for their exclusive species (84–96 %) and also for shared species with *N. pumilio* forests (87–96 %). Mixed forests of *N. pumilio* and *N. betuloides* presented comparably low values of explained information for their exclusive species (70–91 %) and for species shared with *N. pumilio* forests (76–99 %). The five generalist species shared among all three forest types had intermediate values (79–94 %) with lowest values for the fern (*Blechnum penna-marina*) and highest for *Osmorhiza chilensis*, the most common understory species of Tierra del Fuego. The evaluation indices for the indicator species fit similarly than those described before. Boyce index varied from 0.18 to 0.96, P(B = 0) from 0.04 to 0.70, Bcont(20) from -0.27 to 0.88, AVI from 0.28 to 0.57 and CVI from 0.04 to 0.51 (Table 6).

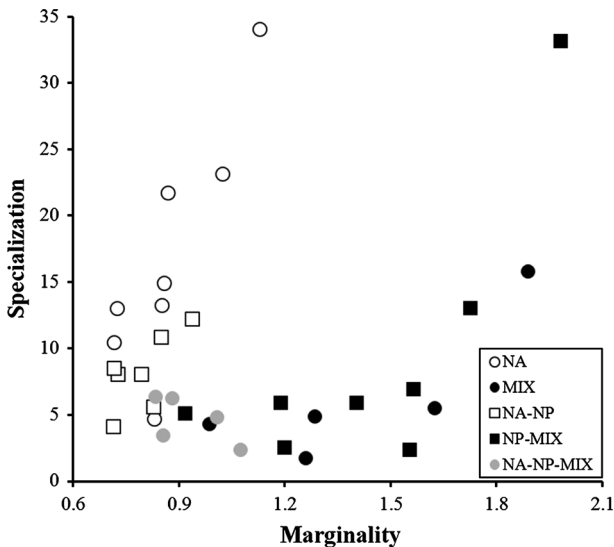


Fig. 3 Specialization (low species' variance compared to global variance of all sites) versus marginality (large difference of species' mean compared to the mean of all sites) of the studied species, classified according to their forest habitat occurrence, NA = *Nothofagus antarctica* forests, NP = *N. pumilio* forests, MIX = mixed forests

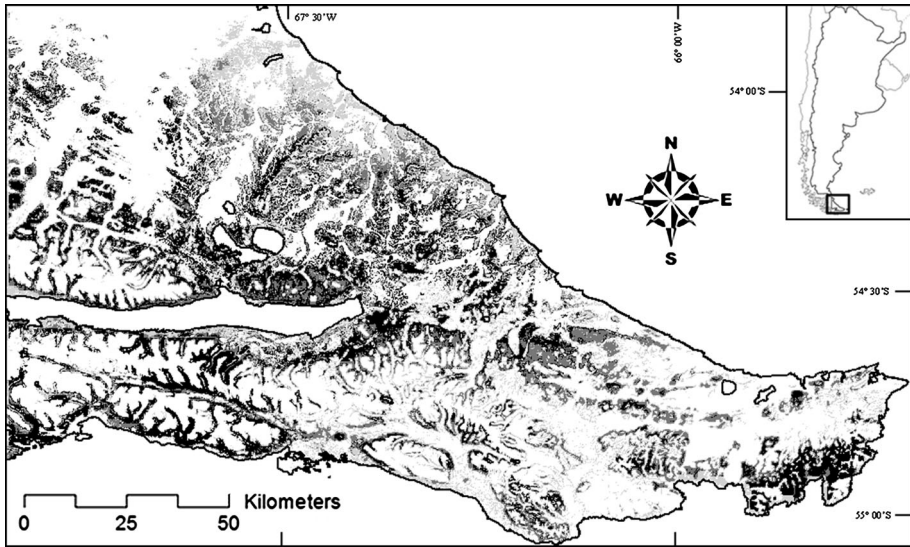


Fig. 4 Map of potential biodiversity (MPB) of the fuegian forests. Low potential = *pale grey*, medium potential = *grey*, high potential = *black*

The marginality and the specialization of the understory plant species presented a pattern that was closely related with the different forest types (Fig. 3). In the marginality/specialization graph it is possible to identify two groups of understory plants, one related to pure deciduous forests (*N. antarctica* and *N. pumilio*) and the other related to mixed deciduous-evergreen forests. Understory plants of deciduous forests show low marginality and vary in specialization, as exclusive plants of *N. antarctica* showed greater specialization than those shared with *N. pumilio* forests. Understory plants of the third group of forests, i.e. mixed forests of deciduous *N. pumilio* and evergreen *N. betuloides* forests showed consistently higher values of marginality, specialization being rather low in most cases. Finally, the generalist plants showed low marginality and low specialization and occupied an intermediate position between both groups.

The map of potential biodiversity (MPB) showed different distribution patterns (Fig. 4) according to the three forest types (Fig. 5). The maps were classified according to the pixel value in three classes: (i) high = 50–100, (ii) middle = 42–50, and (iii) low 1–42. The limits were set so that the three classes contained an identical quantity of pixels. *Nothofagus antarctica* forests with the greatest potential to conserve biodiversity (black) were related to the ecotone areas with *N. pumilio* forests in the southern area of its distribution and with some large isolated patches surrounded by grassland at the central area of the Island. The potential of these forests decreased with the closeness of the Atlantic Ocean. *Nothofagus pumilio* forests with the greater potential were also related to the ecotone areas with *N. antarctica* forests in the flat zones of its distribution at the central-east of the study area. The potential biodiversity of this forest types generally increased from south-west to north-east. Finally, the areas with greatest potential for biodiversity in mixed forests were related to rainfall distribution, mainly in the lower altitudes at the south-west of the study area and at the eastern forests of Tierra del Fuego Island close to Mitre peninsula.

The classification of the potential for biodiversity (Figs. 4, 5) was closely related to the climate and topographic values (Table 3). *Nothofagus antarctica* forests occurred in areas with relatively high temperatures (4.8–5.1 °C compared to 4.6 °C mean temperature for whole Tierra del Fuego) at lower altitudes (103–164 m.a.s.l.), and regulated by the rainfall availability (at least 383 ± 27 mm year⁻¹). The potential of biodiversity in these forests decreased with the annual mean temperature (AMT), and increased with annual precipitation (AP), precipitation of the warmest quarter (PWQ), the global aridity index (GAI where higher values means less arid) and altitude (ALT). *Nothofagus pumilio* forests occurred at lower annual mean temperatures (4.1–4.3 °C) than *N. antarctica* forests, supporting also lower minimum temperatures of coldest month (MINCM). These forests also required higher values of precipitation (AP: 462–476 mm year⁻¹) than *N. antarctica* forests and occurred at higher altitudes in the bottom part and glacier valleys of the mountains (248–301 m.a.s.l.). Their potential biodiversity decreased with AMT, and increased with AP, PWQ, GAI and ALT. Mixed forests occurred at annual mean temperatures (3.9–4.5 °C) comparable to *N. pumilio* forests, but with higher precipitation (AP: 495–543 mm year⁻¹) at lower altitudes (182–297 m.a.s.l.). Their potential of biodiversity also decreased with AMT, and increased with AP, PWQ, GAI and ALT.

Table 3 Mean (SD) of climatic and topographic variables classified according to the potential biodiversity conservation values (Low, Middle, High) for the whole Tierra del Fuego Island (Argentina) and each forest type

Variable	Tierra del Fuego		<i>Nothofagus antarctica</i>			
	Low	Middle	Low	Middle	High	
AMT	4.6 (1.1)		5.1 (0.3)	5.0 (0.2)	4.8 (0.3)	
MAXWM	13.2 (1.3)		12.7 (0.8)	14.0 (0.2)	12.7 (0.6)	
MINCM	-2.5 (1.1)		-2.1 (0.3)	-2.1 (0.3)	-2.3 (0.3)	
AP	452.8 (97.0)		382.6 (26.6)	390.6 (15.7)	412.1 (23.6)	
PWQ	126.4 (24.5)		107.3 (7.3)	129.3 (11.9)	144.5 (10.0)	
EVTP	553.8 (26.7)		577.1 (8.8)	550.7 (20.2)	549.7 (13.2)	
GAI	0.82 (0.22)		0.65 (0.08)	0.68 (0.04)	0.72 (0.04)	
ALT	217.7 (208.3)		103.2 (51.2)	127.9 (44.7)	163.7 (55.9)	
Variable	<i>Nothofagus pumilio</i>			Mixed forests		
	Low	Middle	High	Low	Middle	High
AMT	4.3 (0.9)	4.1 (0.7)	4.1 (0.6)	4.5 (0.6)	4.4 (0.6)	3.9 (0.7)
MAXWM	12.9 (0.9)	14.2 (0.4)	12.9 (0.6)	12.7 (0.7)	13.7 (0.3)	12.3 (0.6)
MINCM	-2.7 (0.8)	-2.9 (0.7)	-2.9 (0.5)	-2.7 (0.6)	-2.8 (0.6)	-3.1 (0.7)
AP	462.1 (54.6)	471.1 (51.9)	476.1 (58.3)	495.4 (39.7)	501.4 (42.7)	542.8 (51.3)
PWQ	110.1 (5.0)	130.4 (10.6)	145.1 (10.3)	115.0 (4.9)	130.6 (11.4)	151.3 (11.5)
EVTP	573.0 (6.0)	546.2 (16.8)	546.2 (13.0)	566.1 (6.8)	545.2 (15.9)	535.5 (14.0)
GAI	0.84 (0.13)	0.86 (0.11)	0.87 (0.12)	0.85 (0.17)	0.92 (0.09)	1.01 (0.11)
ALT	248.3 (161.1)	292.5 (132.7)	301.0 (109.0)	182.2 (127.4)	224.1 (124.2)	297.0 (134.4)

AMT annual mean temperature (°C), MAXWM max temperature of warmest month (°C), MINCM min temperature of coldest month (°C), AP annual precipitation (mm year⁻¹), PWQ precipitation of warmest quarter (mm year⁻¹), EVTP global potential evapo-transpiration (mm year⁻¹), GA global aridity index, ALT altitude (m.a.s.l.)

Discussion

The interest to understand the mechanisms that govern species richness and composition increased during the last decades (Tilman 1994; Tittensor et al. 2014). In this context, niche theories argue that species richness and composition are driven by environmental heterogeneity and adaptations of species (Tokeshi and Schmid 2002). The requirement-based concept of the ecological niche (Grinnell 1917) defines it as a function that links the fitness of individuals to the environment that they inhabit (Hirzel and Le Lay 2008; Allouche et al. 2008). In this framework, habitat suitability models (HSM) predict the occurrence of species based on environmental variables (Guisan and Zimmermann 2000) and define the ecological niche of the species (Hirzel and Le Lay 2008). The strength of the distribution-niche link depends on the ecology, the local constraints, and the historical events within the area (Pulliam 2000). HSM-based studies have traditionally addressed the niche issues of single species, and few studies have yet addressed issues of species assemblage (Hirzel and Le Lay 2008). In this proposal, we combine HSMs of several single species to characterize the understory plant species assemblage of different forest types in Tierra del Fuego. Using a traditional approach (cover and frequency of occurrence) (D'Amato et al. 2009) we selected the most important species for each forest type. These forest types followed a rainfall gradient (north–south) and plant species showed a strong correlation with this gradient, e.g. northern and centre forest types (*N. antarctica* and *N. pumilio*) presented similar assemblage sharing some species, while centre and southern forest types (pure *N. pumilio* and mixed *N. pumilio* - *N. betuloides*) also presented similar assemblage but sharing other species (Table 1). The Ecological Niche Factor Analysis (ENFA) (Hirzel et al. 2002) used here to define HSM, provides factors directly related to the species niche, as marginality and specialization. The marginality indicates in this context how far, all descriptors being accounted for, the species optimum differs from the average conditions in the study area and specialization indicates the species' niche breadth (a high value indicates a narrow niche breadth in comparison with the available conditions) (Hirzel et al. 2002, 2004b; Hirzel and Le Lay 2008; Calenge et al. 2008). Plant species that occurred in northern areas (with dry season and high mean temperatures) presented lower marginality, while plant species that occurred in southern areas (with high rainfall and lower mean temperatures) had higher marginality. These values showed that mixed forests are the ecosystems with highest climate differences according to the average environmental conditions of Tierra del Fuego Island. Specialization was higher for species from *N. antarctica* forests (dry areas) than *N. pumilio* forests (moist areas), a pattern implying that understory species of *N. antarctica* forests presented narrower environmental niches (Table 3).

Identifying the key environmental variables that determine the niche is one of the most crucial HSM operations (Hirzel and Le Lay 2008). The selection of variables often relies on expert stakeholder knowledge (Guisan and Zimmermann 2000), who determine the lower combination of variables produces the best fit to the data (Johnson et al. 2006). Organisms usually respond to a complex of interdependent factors that consist of many environmental variables (Rydgren et al. 2003), where plants with similar ecological requirements usually occur together (Carpenter et al. 2009). Grinnell (1917) listed the factors that potentially affect the species distribution, e.g. vegetation, food, climate, soil, breeding and refuge sites, interspecific effects, and species preferences. However, it is very difficult to find availability of those variables in remote areas such as Southern Patagonia (Martínez Pastur et al. 2015). Remote sensing and geographical information system (GIS) technologies provide a wide spectrum of coarse spatial information that assist in the

evaluation of macro-distribution of species (such as climate, topography and land-cover) (Estrada-Peña and Venzal 2007; Hirzel and Le Lay 2008). In this study, we used climatic variables (e.g. WorldClim) (Hijmans et al. 2005), as factors that drive species' distribution (Guisan and Zimmermann 2000) with a direct influence on the response and physiology of plant species, which cannot evade adverse weather by sheltering or migrating (Hirzel and Le Lay 2008; Allouche et al. 2008). We employed seven variables related to the average and extreme values along the seasons, as well as some climate indexes (Zomer et al. 2008). Topography variables were employed, because they affect species indirectly through correlation with temperature and rainfall, but are often also related to landscape diversity. We used altitude and slope that mainly affect local conditions of light, wetness, temperature and soil type (Guisan et al. 1998). Finally, land-cover data and landscape metrics were employed (six variables), because they determine habitat composition and configuration (e.g. Sachot et al. 2003; Seoane et al. 2004; Braunisch and Suchant 2007; Hirzel and Le Lay 2008; Schindler et al. 2013; Bajocco et al. 2016).

Presence-only methods using ENFA (Hirzel et al. 2002) were largely used for several studies around the World (e.g. Braunisch and Suchant 2007; Estrada-Peña and Venzal 2007; Jiménez Valverde et al. 2008; Allouche et al. 2008; Lachat and Büttler 2009; Poirazidis et al. 2011; Bajocco et al. 2016). ENFA calculates a measure of habitat suitability based on an analysis of marginality (how the species' mean differs from the mean of all sites in the study area) and environmental tolerance (how the species' variance compares with the global variance of all sites) (Allouche et al. 2008). This is an easy methodology to be applied in areas with low data availability such as Southern Patagonia, defining the habitat suitability maps (HSM) for individual species. Here, we propose to combine the individual HSM in one single map, combining different species outputs to generate indicators of potential biodiversity. Numerical composite indices are a combination of several species in one numerical index, e.g. the European farmland bird index that is computed based on population trends of common bird species of agricultural land (Gregory et al. 2005), being included in Structural and Sustainable Development Indicators (EUROSTAT 2008). Spatial composite indices that combine detailed information for several species in a spatial explicit way were only previously developed in few local case studies (e.g. Poirazidis et al. 2011).

Most of temperate forests are not globally threatened in terms of area coverage (MEA 2005; Sedjo et al. 1998), but the use and management modify biodiversity conservation values (Lindenmayer et al. 2012), affecting its capacity to provide the original wide range of ecosystem services (Luque et al. 2011). Several efforts to address forest management practices into a sustainable framework have been made in the last decades (Smith et al. 2006), including a wide array of instruments originated from public and private sectors, such as regulatory policies, economic incentives, information programmes, and market strategies (e.g., certification processes) (Gamondés et al. 2016). In Argentina, recent regulatory changes related to native forest management have been introduced with the passing of National Law 26331/07. This new law and its Regulatory Decree (2009) introduces the payment for the ecosystem services maintenance in managed and non-managed areas, establishing the minimum standards that native forests have to maintain (Gamondés et al. 2016). In practice, each province defines which portion of forests need protection for special conservation values (red status), those managed under sustainable practices (yellow status), and which forests can be converted for other productive purposes such as croplands or plantations (green status). However, this land categorization was defined without any consideration of the special conservation status of the forests, and most protected forests

were simply placed into unproductive or isolated areas without any commercial interest. According to our results, the current categorization under the national law only protects 45 % of those forests with the greatest potential for biodiversity, mainly belonging to mixed and *N. pumilio* forests. However, almost entirely unprotected remain the most valuable areas of *N. antarctica* forests (Martínez Pastur et al. 2012).

Valuing the contribution of ecosystems to human well-being demands robust methods to define and quantify the ecosystem services (e.g. cultural ecosystem services in Patagonia proposed by Martínez Pastur et al. 2015). Decision making and policy aimed at achieving sustainability goals that can be met by applying accurate and defensible methods for quantifying ecosystem services (McKenzie et al. 2011; Crossman et al. 2013). In this sense, spatially explicit units are needed to quantify ecosystem services because their supply and demand are spatially explicit (Nelson et al. 2009). Biodiversity maps can be a potential tool for the design of management and conservation strategies. These maps allowed to cover the geographical heterogeneity of supply and demand of different services (Bastian et al. 2012). Hence, mapping is a useful tool for illustrating and quantifying the spatial mismatch between ecosystem services delivery and demand that can then be used for communication and support decision-making (Braunisch and Suchant 2007; Nelson et al. 2009; Crossman et al. 2013).

Conclusions

Habitat suitability models developed with indicator species were very effective to develop a decision support system for conservation and management strategies at different landscape levels. These models allow us to develop a map of potential biodiversity (MPB), which was related to climate, topographic and forest pattern metrics variables. The MPB can contribute greatly: (i) to delineate the ecological requirements of species and their limiting factors; (ii) to understand biogeography and dispersal barriers; (iii) to design conservation plans and reserves; (iv) to predict effects of habitat loss; and (v) to predict climate change effects (Peterson 2006). Another advantage of the proposed MPB maps was the identification of biodiversity hotspots, understanding this concept as an area with greater species richness compared to surrounding areas (Lachat and Büttler 2009). Thus, the map allows to identify forests with different conservation potential across the landscape, and can be used to identify land-use conflicts, e.g. timber production, livestock and inadequate conservation effort within the current system of Natural Reserves.

Acknowledgments This research was supported by the MINCYT-BMWF Cooperation Programme (2013–2015) through the project: “Environmental niche factor analysis (ENFA) for developing conservation maps with emphasis in vegetation diversity for Tierra del Fuego, Argentina”. This paper was also written with the financial support of the “Operationalisation of Ecosystem Services and Natural Capital: From concepts to real-world applications (OpenNESS)” project financed under the European Commission’s Seventh Framework Programme (Project number 308428).

Appendix

See Fig 5, Tables 4, 5 and 6.

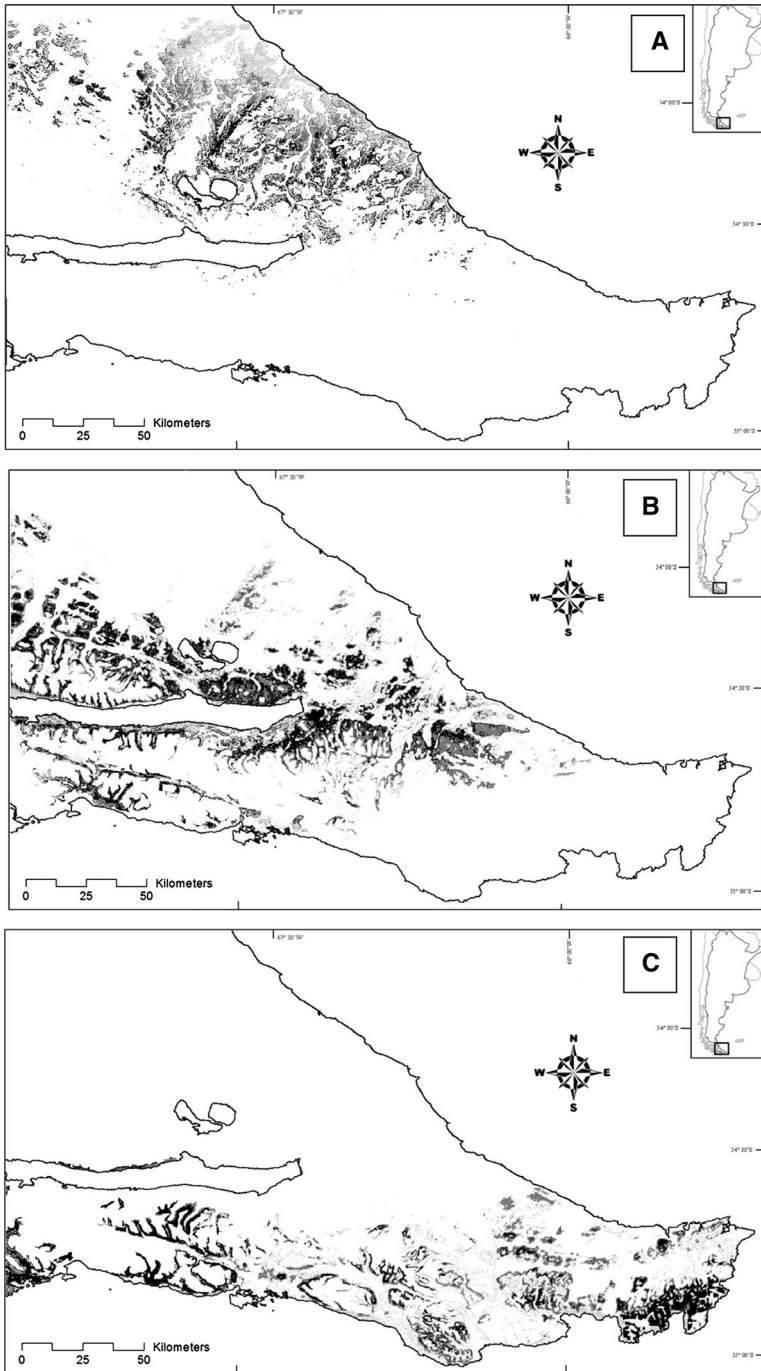


Fig. 5 Biodiversity maps (BM) for different Fuegian forest types (A = *Nothofagus antarctica*, B = *N. pumilio*, C = mixed forests). Low potential = pale grey, medium potential = grey, high potential = black

Table 4 Correlation among variables

Variable	MAXWM	MINCM	AP	PWQ	EVTP	GAI	ALT	SLO	ED	LPI	PL_NA	PL_NP	PL_MF	PLAND
AMT	0.888	0.758	-0.388	-0.404	0.567	-0.570	-0.778	-0.595	-0.055	-0.116	0.142	-0.134	-0.139	-0.112
MAXWM		0.411	-0.119	-0.185	0.699	-0.339	-0.511	-0.437	-0.025	-0.070	0.171	-0.066	-0.180	-0.065
MINCM			-0.731	-0.687	0.153	-0.765	-0.852	-0.604	-0.110	-0.160	0.097	-0.176	-0.119	-0.161
AP				0.905	0.028	0.919	0.591	0.465	0.029	0.081	-0.194	0.106	0.171	0.079
PWQ					0.069	0.900	0.548	0.439	0.062	0.103	-0.204	0.093	0.236	0.103
EVTP						-0.033	-0.277	-0.263	0.032	0.006	0.125	0.001	-0.101	0.012
GAI							0.705	0.553	0.004	0.064	-0.224	0.100	0.177	0.059
ALT								0.633	-0.025	0.063	-0.166	0.157	0.043	0.056
SLO									0.009	0.165	-0.154	0.148	0.198	0.154
ED										0.439	0.375	0.179	0.211	0.500
LPI											0.373	0.642	0.396	0.992
PL_NA												-0.125	-0.157	0.392
PL_NP													-0.166	0.636
PL_MF														0.399

AMT annual mean temperature (°C), MAXWM max temperature of warmest month (°C), MINCM min temperature of coldest month (°C), AP annual precipitation (mm year⁻¹), PWQ precipitation of warmest quarter (mm year⁻¹), EVTP global potential evapo-transpiration (mm year⁻¹), GAI global aridity index, ALT altitude (m.a.s.l.), SLO slope (%), ED edge density (m ha⁻¹), LPI largest patch index (ha), PL_NA landscape with *Nothofagus antarctica* forests (%), PL_NP landscape with *N. pumilio* forests (%), PL_MF landscape with mixed forests (%), PLAND landscape with forests (%)

Table 5 Eigenvalues and percentage of explained information for the first three axes

Species	E1	E2	E3	Total
ACMA	11.65 (0.05)	164.52 (0.71)	25.20 (0.11)	(0.87)
ACOV	158.18 (0.36)	247.24 (0.57)	13.66 (0.03)	(0.96)
ADCH	50.21 (0.10)	348.33 (0.71)	39.80 (0.08)	(0.89)
BEBU	6.72 (0.04)	108.59 (0.66)	22.16 (0.13)	(0.83)
BLPE	6.25 (0.08)	35.89 (0.47)	18.87 (0.24)	(0.79)
BRUN	634.63 (0.20)	1713.93 (0.55)	550.45 (0.18)	(0.93)
CAGL	261.46 (0.47)	223.99 (0.41)	34.07 (0.06)	(0.94)
CEAR	1141.62 (0.47)	738.41 (0.30)	448.61 (0.18)	(0.95)
CHDI	90.96 (0.27)	162.66 (0.49)	48.43 (0.15)	(0.91)
COLE	2812.56 (0.81)	370.44 (0.11)	161.51 (0.05)	(0.97)
COSC	25.96 (0.09)	193.95 (0.64)	32.08 (0.11)	(0.84)
DEFL	692.25 (0.29)	1187.34 (0.50)	345.26 (0.15)	(0.94)
DYGL	173.27 (0.36)	235.94 (0.48)	34.15 (0.07)	(0.91)
EMRU	136.99 (0.38)	156.26 (0.43)	35.29 (0.10)	(0.91)
FEMA	412.97 (0.46)	285.42 (0.31)	140.89 (0.16)	(0.93)
GAAP	677.32 (0.33)	771.74 (0.37)	502.54 (0.24)	(0.94)
GAFU	4032.06 (0.61)	1501.29 (0.23)	693.01 (0.11)	(0.95)
GUMA	4.98 (0.06)	38.01 (0.48)	17.68 (0.22)	(0.76)
MAGR	78.49 (0.19)	134.44 (0.32)	124.95 (0.30)	(0.81)
OSCH	100.58 (0.31)	177.64 (0.55)	26.63 (0.08)	(0.94)
OSDE	224.43 (0.40)	251.68 (0.44)	40.87 (0.07)	(0.91)
PEMU	2032.60 (0.86)	246.66 (0.10)	59.59 (0.03)	(0.99)
PEPU	122.83 (0.47)	82.28 (0.31)	29.14 (0.11)	(0.89)
PHAL	378.51 (0.42)	318.00 (0.35)	132.14 (0.15)	(0.92)
RIMA	6.62 (0.15)	18.09 (0.42)	5.42 (0.13)	(0.70)
RUGE	251.52 (0.37)	265.23 (0.39)	92.46 (0.14)	(0.90)
SCRA	1079.19 (0.71)	197.23 (0.13)	167.63 (0.11)	(0.95)
SEAC	4805.89 (0.96)	334.04 (0.02)	144.89 (0.01)	(0.99)
TAGI	696.74 (0.09)	5973.92 (0.80)	529.64 (0.07)	(0.96)
TRSP	541.49 (0.53)	245.59 (0.24)	163.86 (0.16)	(0.93)
UNLE	1090.50 (0.67)	407.14 (0.25)	64.33 (0.04)	(0.96)
VIMA	4323.95 (0.27)	7567.19 (0.47)	3650.49 (0.22)	(0.96)
VOMA	10.43 (0.11)	41.06 (0.45)	21.17 (0.23)	(0.79)

Value (Expl. Spec.). Species codes are presented in Table 1

Table 6 Statistics for the adjustment of the map models

Species	B	P(B = 0)	Bcont(20)	AVI	CVI
ACMA	0.52 (0.74)	0.16 (0.09)	0.20 (0.69)	0.50 (0.23)	0.20 (0.22)
ACOV	0.96 (0.09)	0.04 (0.09)	0.64 (0.30)	0.51 (0.15)	0.34 (0.12)
ADCH	0.64 (0.33)	0.36 (0.33)	0.37 (0.22)	0.30 (0.08)	0.24 (0.05)
BEBU	0.24 (0.43)	0.60 (0.25)	-0.27 (0.21)	0.43 (0.24)	0.04 (0.25)
BLPE	0.25 (0.94)	0.13 (0.12)	0.03 (0.78)	0.28 (0.20)	0.07 (0.29)

Table 6 continued

Species	B	P(B = 0)	Bcont(20)	AVI	CVI
BRUN	0.55 (0.48)	0.36 (0.32)	0.38 (0.42)	0.60 (0.27)	0.51 (0.26)
CAGL	0.64 (0.44)	0.36 (0.44)	0.36 (0.34)	0.50 (0.24)	0.25 (0.19)
CEAR	0.54 (0.37)	0.46 (0.37)	0.15 (0.47)	0.42 (0.26)	0.11 (0.23)
CHDI	0.84 (0.26)	0.16 (0.26)	0.72 (0.42)	0.52 (0.14)	0.46 (0.12)
COLE	0.36 (0.36)	0.56 (0.22)	0.26 (0.18)	0.46 (0.17)	0.39 (0.14)
COSC	0.52 (0.36)	0.48 (0.36)	0.12 (0.42)	0.52 (0.18)	0.33 (0.16)
DEFL	0.28 (0.36)	0.64 (0.26)	−0.12 (0.44)	0.35 (0.14)	0.01 (0.16)
DYGL	0.56 (0.33)	0.44 (0.33)	0.35 (0.42)	0.47 (0.19)	0.30 (0.16)
EMRU	0.92 (0.11)	0.08 (0.11)	0.62 (0.18)	0.45 (0.06)	0.27 (0.03)
FEMA	0.80 (0.25)	0.20 (0.25)	0.44 (0.51)	0.55 (0.22)	0.36 (0.20)
GAAP	0.80 (0.35)	0.20 (0.35)	0.67 (0.32)	0.49 (0.09)	0.37 (0.08)
GAFU	0.64 (0.48)	0.28 (0.30)	0.28 (0.37)	0.57 (0.21)	0.47 (0.20)
GUMA	0.96 (0.09)	0.04 (0.08)	0.88 (0.14)	0.50 (0.21)	0.46 (0.20)
MAGR	0.86 (0.30)	0.14 (0.30)	0.74 (0.21)	0.54 (0.15)	0.50 (0.14)
OSCH	0.72 (0.30)	0.28 (0.30)	0.57 (0.25)	0.48 (0.22)	0.28 (0.20)
OSDE	0.72 (0.30)	0.28 (0.30)	0.42 (0.42)	0.54 (0.23)	0.36 (0.20)
PEMU	0.68 (0.18)	0.32 (0.18)	0.40 (0.30)	0.55 (0.22)	0.49 (0.20)
PEPU	0.80 (0.24)	0.20 (0.24)	0.58 (0.16)	0.53 (0.22)	0.26 (0.15)
PHAL	0.76 (0.22)	0.24 (0.22)	0.47 (0.36)	0.52 (0.20)	0.33 (0.19)
RIMA	0.92 (0.11)	0.08 (0.11)	0.68 (0.21)	0.55 (0.18)	0.46 (0.13)
RUGE	0.86 (0.31)	0.14 (0.31)	0.80 (0.24)	0.54 (0.13)	0.49 (0.11)
SCRA	0.80 (0.24)	0.20 (0.24)	0.51 (0.28)	0.55 (0.20)	0.30 (0.16)
SEAC	0.68 (0.50)	0.24 (0.33)	0.50 (0.26)	0.50 (0.12)	0.47 (0.11)
TAGI	0.22 (0.46)	0.70 (0.40)	−0.15 (0.38)	0.43 (0.27)	0.24 (0.24)
TRSP	0.76 (0.33)	0.24 (0.33)	0.54 (0.34)	0.52 (0.12)	0.32 (0.11)
UNLE	0.88 (0.11)	0.12 (0.11)	0.57 (0.35)	0.54 (0.19)	0.38 (0.15)
VIMA	0.18 (0.57)	0.51 (0.27)	0.07 (0.44)	0.50 (0.31)	0.39 (0.29)
VOMA	0.84 (0.09)	0.16 (0.09)	0.74 (0.16)	0.52 (0.20)	0.39 (0.16)

B Boyce index, *P(B = 0)* proportion of validation points, *Bcont(20)* continuous Boyce index, *AVI* absolute validation index, *CVI* contrast validation index. Mean (SD). Species codes are presented in Table 1

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