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ORIGINAL PAPER

Potential biodiversity map of darkling beetles (Tenebrionidae): environmental characterization, land-uses and analyses of protection areas in Southern Patagonia

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Abstract

Different methodologies had been developed for species management and conservation based on modelling of potential biodiversity at regional scales. However, most of these models were fitted for umbrella species (e.g. big mammals) rather than micro-fauna. Beetles should be included to improve conservation strategies due to their functional roles and vulnerability in arid environments. The maps of potential biodiversity (MPB) based on different potential habitat suitability (PHS) maps are useful to indicate high biodiversity areas. Firstly, we aim to elaborate a MPB of darkling beetles (Coleoptera: Tenebrionidae) based on 10 species PHS maps inhabiting Santa Cruz Province (Argentina). Then, we analysed the MPB an environmental gradients and land-use variables. We explored 41 potential variables to develop PHS maps. The MPB was included into a GIS project, and was analysed considering climatic and topographic variables, ecological areas and soil organic carbon (SOC) stock, also sheep density, desertification and protected area network. The modelled showed great variability in their habitat requirements (e.g. temperature), where marginality (PHS differs from the available conditions) and specialization (environmental condition range of PHS) determined three species groups. MPB increased from grasslands in the NE to shrublands in the SE, and was higher with SOC, sheep density and desertification degree. Protection areas included lower MPB for darkling beetles, where provincial reserves have a major conservation role compared with national parks. MPB allowed us to understand the potential trade-offs with the environment and human uses. This gave us a tool to development new strategies (e.g. land-sparing) for management and conservation.

Keywords Habitat suitability · Landscape scale · Marginality/specialization · Trade-offs · Conservation

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Introduction

Several methodologies and software were developed to define habitat modelling at global and regional scales (e.g. MaxEnt and Biomapper; Hirzel et al. 2001; Phillips et al. 2006; Rodríguez et al. 2007). These models describe the relationships between environmental characteristics (climatic, topographic and landscape variables) and the occurrence of species in a particular area (Guisan and Zimmermann 2000; Hirzel et al. 2002; Soberón and Peterson 2005; Elith and Leathwick 2009). Most of these studies were conducted for umbrella species (mainly for big mammals or emblematic birds) in areas with a large quantity of reliable long-term data and available environmental cartography (Rodríguez et al. 2007). The modelling of potential habitat of inconspicuous species (e.g. insects) is necessary for a more effective biodiversity conservation (Buse et al. 2007; Samways 2007; Tognelli et al. 2009; Bosso et al. 2018). Models of habitat species distribution were fitted for darkling beetles elsewhere, and they were useful for studies about: (i) ecology of the species (Buse et al. 2007), (ii) climatic change and habitat modification in future scenarios or past climatic conditions (Homburg et al. 2014), and (iii) potential geographic distribution in new or unexplored regions (Bosso et al. 2018). These models also can be applied to determine the requirements of individual species. During the last few years several studies had been conducted in areas with scarce data based mainly on remote sensing, and maps of potential biodiversity (MPB) by combining potential habitat suitability (PHS) maps of different taxa (Martínez Pastur et al. 2016; Rosas et al. 2018). MPB can synthetize the information of several species, allowing to define better management and conservation planning, as well as to assess the effectiveness of the current networks of protected areas (Rosas et al. 2018).

Darkling beetles are abundant in arid and semiarid environments (Matthews et al. 2010) such as in Patagonia, where ecological information for these groups were limited (Carrara and Flores 2013). In this area, 122 species of Tenebrionidae were listed (Carrara and Flores 2015) mainly belonging to subfamilies Pimeliinae (tribes Nycteliini, Praociini and Trilobocarini) and Tenebrioninae (tribe Scotobiini) (Sackmann and Flores 2009; Carrara and Flores 2013). Patagonian steppe presents high endemism at species level of darkling beetles (Carrara and Flores 2013). Tenebrionidae was the most studied group due to their vulnerability and extinction risks, where available information were related to their general ecology, endemism check-lists, and biogeography (Mazia et al. 2006; Domínguez et al. 2006; Ruggiero et al. 2009; Sackmann and Flores 2009; Carrara et al. 2011a, b; Carrara and Flores 2013, 2015; Lescano et al. 2017). Southern Patagonia presents different landscapes with extreme environmental conditions, from arid steppes to dense temperate forests (Peri et al. 2016), and with different levels of natural and human impacts (e.g. livestock grazing or desertification) that can greatly affect darkling beetles (Newbold et al. 2014; Liu et al. 2016; Li et al. 2018). The objectives of this work were to: (i) elaborate a MPB of darkling beetles (Coleoptera: Tenebrionidae) based on PHS maps of 10 species inhabiting Santa Cruz Province (Argentina) using environmental niche factor analysis (ENFA), and (ii) analyse it performance across environmental and land-use gradients. The hypothesis was that darkling beetles potential biodiversity changed across the environment, climatic and vegetation gradients. Additionally, MPB can be used to detect potential trade-offs with natural and human induced processes (e.g. desertification and livestock), or to test the effectiveness of the current natural reserve networks.

Methods

The study was carried out in Santa Cruz Province (Argentina) (46°00′ to 52°30′S, 66°00′ to 73°00′W), which covers 243,943 km^2 (Fig. 1a). The main ecological areas are dominated by steppe and shrublands, while sub-Andean grasslands, *Nothofagus* forests and alpine vegetation occupy a narrow fringe in the west (Oliva et al. 2004) (Fig. 1b). Soil organic carbon (SOC) stock decreased from South to North, and from forests to dry steppes (Peri et al. 2018) (Fig. 1c). Sheep grazing was one of the main economic activity in the province, where density presented the highest values close to coasts and southern areas (Pedrana et al. 2011) (Fig. 1d). Most of the study area presented a moderately and severely degrees of desertification, while slightly degrees of desertification were associated to the mountains (Del Valle et al. 1998) (Fig. 1e). Finally, national parks mainly preserve forests and ice fields close to the mountains (e.g. Perito Moreno National Park), while provincial reserves mainly protect special features in the steppe landscape (e.g. Punta Gruesa Provincial Reserve) (Fig. 1f).

We elaborated a MPB of darkling beetle (Coleoptera: Tenebrionidae) in Santa Cruz Province following the methodology proposed by Martínez Pastur et al. (2016) and Rosas et al. (2018). We used a database of darkling beetles based on 757 species geographic locations. This database was constructed in base on tenebrionid specimens housed in CEI (Entomological collection of Instituto Argentino de Investigaciones de las Zonas Áridas, IADIZA). Occurrence data were visualized in a GIS project, and we erased repeated record for the same location. Then we selected ten species with the highest occurrence in the province (final occurrence points were presented between brackets): nine were endemic

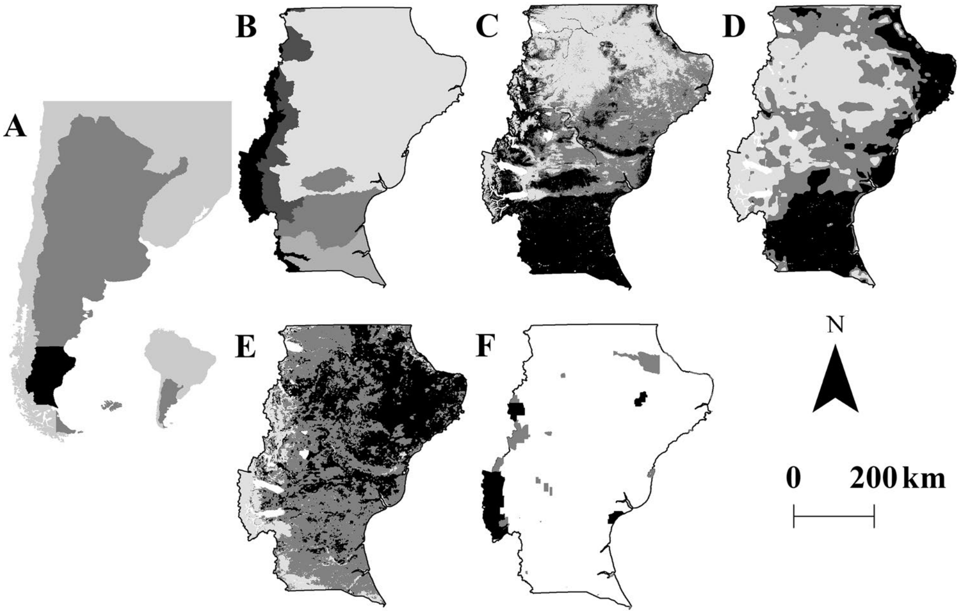

Fig. 1 Characterization of the study area: **a** location of Argentina (dark grey) and Santa Cruz Province (black), **b** main ecological areas (light grey = dry steppe, grey = humid steppe, medium grey = shrublands, dark grey = sub-Andean grasslands, black = forests and alpine vegetation) (modified from Oliva et al. 2004), **c** soil organic carbon (light grey ≤ 4.5, grey = 4.5–5.5, black ≥ 5.5 kg m^{-2}) (Peri et al. 2018), **d** sheep density (light grey ≤ 0.3, grey = 0.3–0.6, black ≥ 0.6 sheep ha^{-1}) (Pedrana et al. 2011), **e** desertification (light grey = slightly, grey = moderately, black = severely) (Del Valle et al. 1998), and **f** protection areas (grey = provincial reserves, black = national parks)

to Patagonian steppe (Carrara and Flores 2015): *Epipedonota lata* Waterhouse (n = 36), *E. tricostata* Burmeister (n = 30), *Nyctelia bremi* Waterhouse (n = 43), *N. corrugata* Curtis (n = 15), *N. darwini* Waterhouse (n = 46), *N. fitzroyi* Waterhouse (n = 14), *N. sallei* Fairmaire (n = 25), *Praocis bicarinata* Burmeister (n = 33) (Pimeliinae subfamily), and *Emmallodera multipunctata* (n = 46) (Tenebrioninae subfamily), and one that is distributed across all Patagonia steppe and adjacent areas, *Mitragenius araneiformis* Curtis (n = 22) (Pimeliinae subfamily) (Tognelli et al. 2009).

Using ENFA (Hirzel et al. 2002), we performed a series of spatially explicit PHS models for each darkling beetle species using Biomapper 4.0 software (Hirzel et al. 2004). ENFA compares the eco-geographical variables distribution for a presence data set consisting of locations where the species has been detected with the predictor distribution of the total study area (Hirzel et al. 2001). Also, ENFA calculated two index: (i) the global marginality (from 0 to 1) where the lower values indicates that the species tends to live in average conditions throughout the study area, and (ii) the global tolerance or specialization (tolerance^{-1}) (from 0 to infinite) where lower values represents a specialist species tending to live in a very narrow range of environment conditions (Hirzel et al. 2002; Martínez Pastur et al. 2016). We used a distance of geometric-mean algorithm to perform PHS maps, which provides a good generalization of the niche characterization (Hirzel and Arlettaz 2003). The resulting PHS maps had scores that varied from 0 (minimum) to 100 (maximum habitat suitability). The model evaluation for these maps elaborated with data presence only was conducted comparing the obtained results with a random model (Hirzel et al. 2006). We evaluated the model using these cross-validation processes through: (i) Boyce index (B) (− 1 to 1) is the Spearman rank correlation on the Fi = Pi/Ei, which measure of the monotonicity of the curve, where *Pi* are validation points and *Ei* is a box (by default, $b = 4$), and where each box covers a portion of the total area. Positive values indicate that the predictions model are consistent with the presences distribution in the evaluation dataset, and values close to zero mean that the model is not different from a random model. Furthermore, negative values indicate an incorrect model. (ii) The continuous Boyce index (Bcont) is defined as the Boyce index based on a moving window. (iii) The proportion of validation points (P) are those observations left out during the cross-validation process (Boyce et al. 2002; Hirzel et al. 2006). (vi) The absolute validation index (AVI) is defined as the proportion of presence evaluation points falling above a fixed PHS threshold (e.g. 0.5) varying from 0 to 1 where higher values indicate trust modelling. And, (v) the contrast validation index (CVI) which is defined as AVI minus the AVI − AVI > 50, and which varying between 0.0 and 0.5 (zero means that model accuracy does not outperform a random model) (Hirzel and Arlettaz 2003; Hirzel et al. 2004). For modelling, we explored 41 potential explanatory variables (Appendix 1), which were rasterized at 90 × 90 m resolution using the nearest resampling technique on ArcMap 10.0 software (ESRI 2011). For further details of climatic, topographic and landscape variables (Del Valle et al. 1998; Hijmans et al. 2005; Farr et al. 2007; ORNL DAAC 2008; Zomer et al. 2008; Zhao and Running 2010; McGarigal et al. 2012; Peri et al. 2018; Rosas et al. 2017, 2018).

PHS maps of each species were visualized in a GIS project with the same resolution of 90 × 90 m, and a mask based on the normalized difference vegetation index (NDVI) was used (less than 0.05) to detect bare soil, ice-fields and water bodies (Lillesand and Kiefer 2000). Finally, the obtained PHS maps (n = 10) were combined (average values for each pixel) and one MPB was obtained for darkling beetles species in Santa Cruz Province. This map had scores that varied from 0 to 68% (average values of PHS for all the studied species), so, it was re-scale by a lineal method from 0 to 100%. For the comparisons, we classified the MPB as: (i) low potential biodiversity (1–30%), (ii) medium potential biodiversity (31–55%), and (iii) high potential biodiversity (56–100%), where the limits were defined into three classes containing an equal quantity of pixels for the entire study area. We characterize these three quality classes through their: (i) climate and topographic variables compared with the whole study area, (ii) the occurrence at different environments, (iii) vegetation and land-use areas, and (iv) the occurrence inside and outside the protected natural areas (national parks and provincial reserves).

Results

Potential habitat suitability maps

For the PHS modelling, we finally selected five environmental variables with the lowest correlation among them, based on the Pearson's correlation index (Appendix 2): annual mean temperature, minimum temperature of the coldest month, annual precipitation, elevation, and NDVI. The Pearson's correlation index varied between 0.25 and 0.85, where the lowest correlation was between annual mean temperature and minimum temperature of coldest month (− 0.25), and the highest values were found between the elevation and the minimum temperature of coldest month (− 0.85), and between elevation and annual precipitation (0.69). The outputs of PHS models explained 100% of the information (average eigenvalues of the first four axes were 198.80 > 68.46 > 7.41 > 2.00) (Appendix 3). Cross-validation indicated that the models presented the following fitting: (i) Boyce index (B) varied between 0.04 and 0.75, (ii) P(B = 0) varied from 0.21 to 0.65, (iii) Bcont(20) varied between − 0.02 and 0.41, (iv) AVI varied between 0.45 and 0.67, and (v) CVI varied between 0.23 and 0.58. The worst performance were obtained for *N. sallei*, where: (i) B = 0.04 indicated that this model is not different from a random model, which is coincident with obtained values of AVI = 0.45 and CVI = 0.23 that indicate the species is a generalist species. The remaining species presented higher values of Boyce index, that indicate these models were consistent with the database, and presented higher values of AVI and CVI, which indicate that models predictions were consistent (Appendix 4).

Marginality and specialization indexes (Fig. 2) allowed to separate the species in three groups: (i) the first group (*N. darwini*, *N. sallei*, *E. lata* and *M. araneiformis*) showed low marginality (0.57–0.65) and specialization (4.96–7.46) values, (ii) a second group (*E. multipunctata*, *P. bicarinata*, *E. tricostata*, *N. bremi* and *N. corrugata*) showed high marginality (0.76–0.89) and low specialization (4.29–8.35) values, and (iii) a third group with a single species (*N. fitzroyi*) presented a medium marginality value (0.74) and the highest specialization value (13.57). PHS maps (Fig. 3) presented different distribution and habitat requirements: (i) in the East, *N. darwini*, *N. sallei*, *E. lata* and *M. araneiformis* presented the highest values of PHS (Fig. 3a–d), (ii) *N. fitzroyi* presented the highest values in the North-East (Fig. 3e), and (iii) in the South the highest values were found for *E. multipunctata*, *P. bicarinata*, *E. tricostata*, *N. bremi* and *N. corrugata* (Fig. 3f–j).

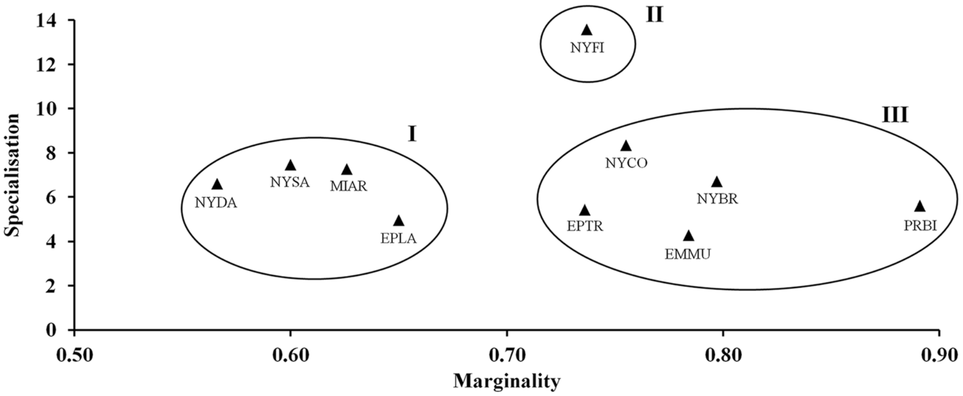

Fig. 2 Specialization (low species' variance compared to global variance of all sites) versus marginality (large difference of species' mean compared to the mean of all sites) of the darkling beetles, grouped according to their similarity. *NYDA Nyctelia darwini*, *NYSA N. sallei*, *NYFI N. fitzroyi*, *NYBR N. bremi*, *NYCO N. corrugata*, *EPLA Epipedonota lata*, *EPTR E. tricostata*, *MIAR Mitragenius araneiformis*, *EMMU Emmallodera multipunctata*, *PRBI Praocis bicarinata*

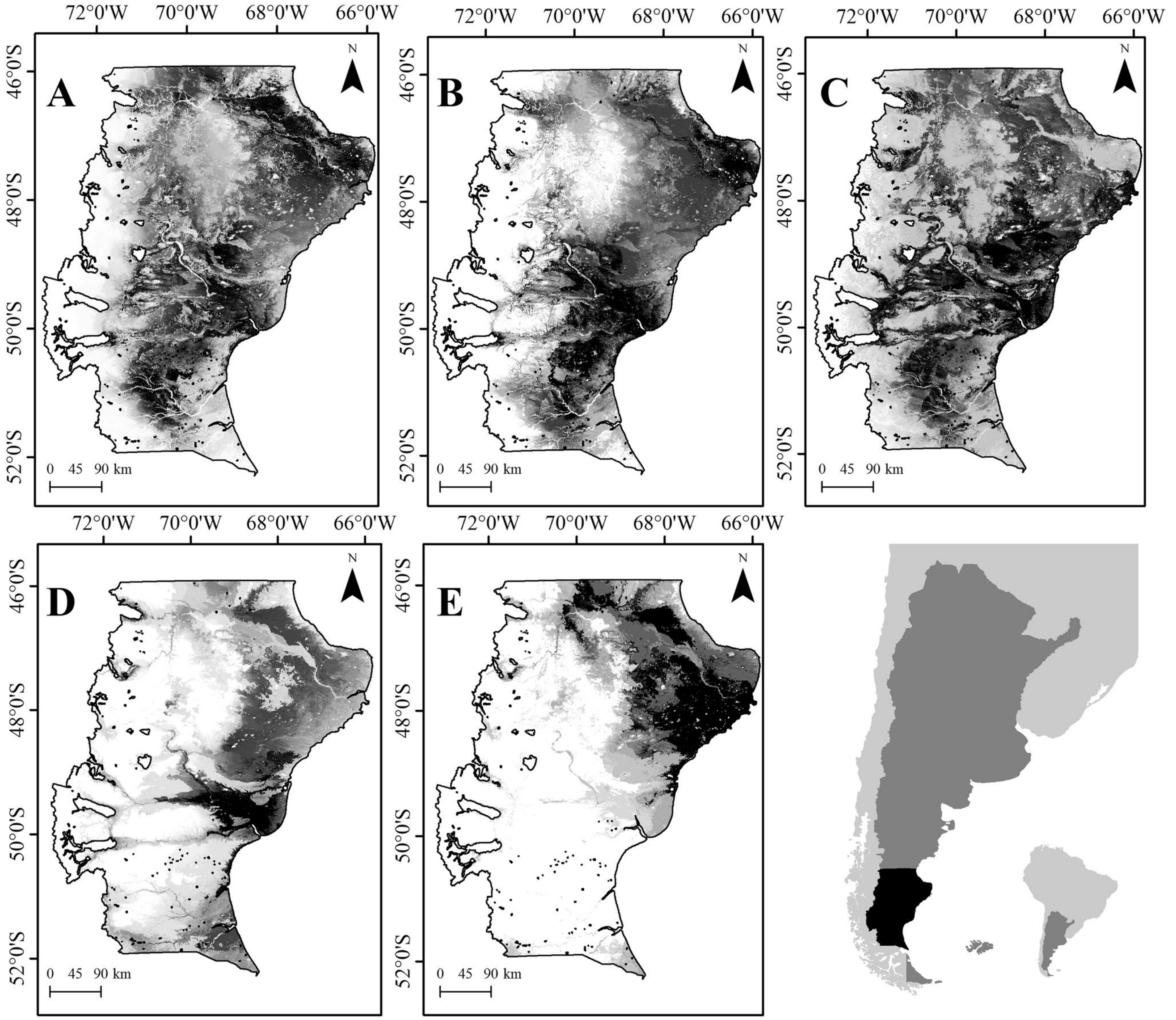

Fig. 3 Potential habitat suitability (PHS) maps of darkling beetles in Santa Cruz Province, where light grey showed the lowest potential and black showed the highest potential areas (0–100%). **a** *Nyctelia darwini*, **b** *Nyctelia sallei*, **c** *Epipedonota lata*, **d** *Mitragenius araneiformis*, **e** *Nyctelia fitzroyi*, **f** *Emmallodera multipunctata*, **g** *Praocis bicarinata*, **h** *Epipedonota tricostata*, **i** *Nyctelia bremi*, *and* **j** *Nyctelia corrugata*

Environmental characterization of the map of potential biodiversity

The combination of the PHS maps of the different species allowed us to obtain a MPB of darkling beetles for the whole study area (Fig. 4), where higher potential biodiversity occurred in the Eastern and South-Eastern areas, and decreased towards a gradient from East to West. Beside this, alluvial valley of the main rivers and the closeness to water bodies (e.g. big lakes near to the Andes Mountains) increased the potential biodiversity, while the closeness to ice-fields and forests decreased it.

The environmental characterization determined that potential biodiversity (from low to medium–high qualities) increased with the temperatures variables (e.g. annual mean temperature), except with the mean temperature of driest quarter (Table 1). Potential biodiversity increased when rainfall related variables decreased (low > medium > high) (e.g. annual precipitation) as well as with topographic variables (elevation and slope). In others rainfall variables, potential biodiversity increased with the variables (e.g. precipitation of driest month), but from low to medium–high, as well as the global aridity index. Finally, potential biodiversity increased when global potential evapo-transpiration

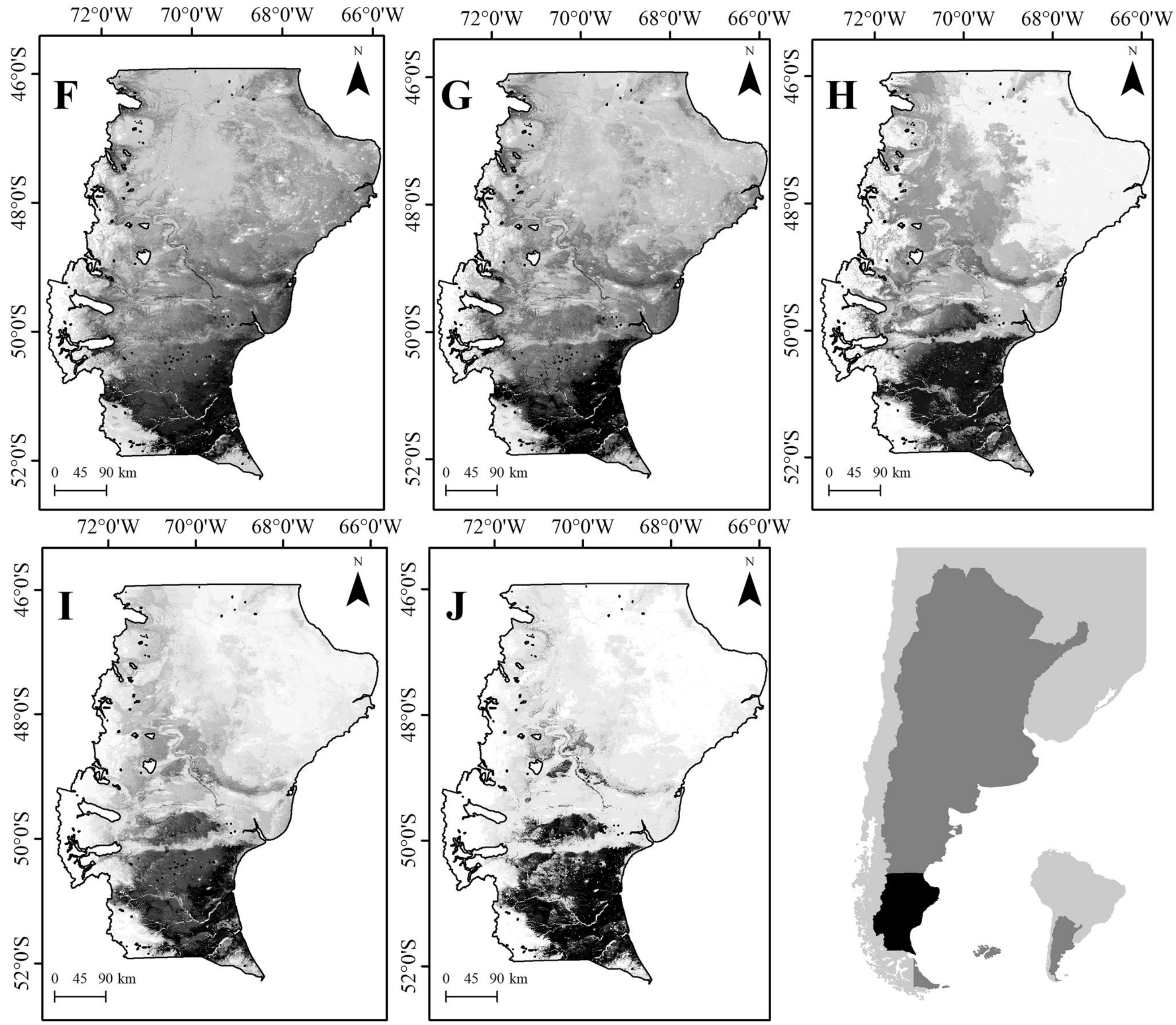

Fig. 3 (continued)

increasing. In general, the higher potential biodiversity occurred in areas with higher temperatures and lower rainfall (semiarid and arid environments) compared to the average of the entire study area, and in areas with lower elevation and slopes (plain landscapes).

NDVI, as a proxy of vegetation, decreased from forests to dry grasslands. NDVI where partially correlated with the climatic variables employed in the modelling (0.58 with annual mean temperature, − 0.55 with min temperature of coldest month, and 0.51 with annual precipitation) (Appendix 2). The ecological areas greatly affected the potential biodiversity quality of darkling beetles (Table 2). The highest qualities were found in shrublands (81% of the area corresponded to high MPB) and humid steppes (58%). These ecological areas represented 20% of the Province. The dry steppe presented the large areas (68% of the study area) and included 43% of medium and 28% of high qualities potential biodiversity categories. Forests, alpine vegetation and sub-Andean grasslands had the lowest values in the MPB (86–100% of the area corresponded to low quality potential biodiversity values). SOC stock also had influenced the MPB (Table 2), where greater SOC showed higher potential biodiversity values (47% of the area with SOC > 5.5 kg m^{-2}). Medium SOC (4.5–5.5 kg m^{-2}) also presented higher potential values (medium 37% and high 42% of the area) compared with low SOC (< 4.5 kg m^{-2}).

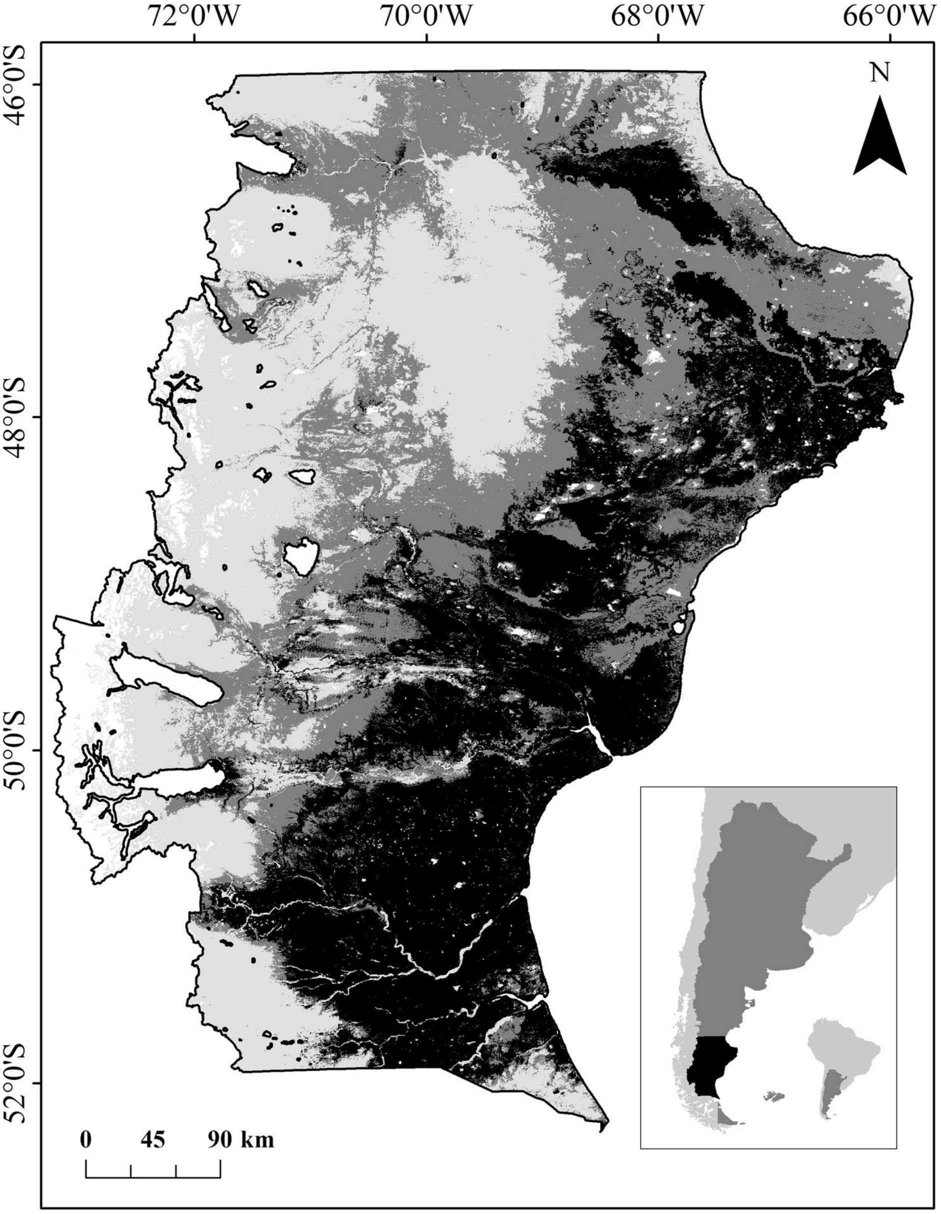

Fig. 4 Map of potential biodiversity of darkling beetles in Santa Cruz Province. Low potential = pale grey (1–30%), medium potential = grey (31–55%), high potential = black (56–100%)

Land-uses and protection status analyses of the map of potential biodiversity

Livestock (sheep density) presented similarities with the MPB (Table 2). Thus, low intensity uses (< 0.3 sheep ha^{-2}) occurred in areas with low potential biodiversity (low 59% and medium 32% of the area), and high intensity uses (> 0.6 sheep ha^{-2}) occurred in areas with high potential biodiversity (medium 25% and high 61% of the area). Desertification processes also showed matches with the MPB (Table 2), where severely impacted areas had the highest potential biodiversity (medium 41% and high 35% of the area), and the slightly impacted areas presented the lowest qualities (low 79% of the area). Finally, when MPB values were analyzed according their protection status, we found that 24.6% of the protected areas (16,451.3 km^2) corresponded to medium–high qualities (40% of medium and 60% of high quality). National parks included 1175.9 km^2 of medium–high qualities (11.8% of the total area) while provincial reserves included 2878.0 km^2 (44.1% of the total area). National parks protected more areas than provincial reserves (× 1.5-fold), however these areas were less valuables to protect darkling beetles.

Table 1 Characterization (mean and standard deviation) of the climatic and topographic variables according to the potential biodiversity map of darkling beetles: total area represent values of the entire province, low potential (1–30%), medium potential (31–55%) and high potential (56–100%) classified according to the modelling

Variable	Total area	Low	Medium	High
Temperature				
Annual mean temperature (°C)	7.76 (2.40)	6.86 (2.50)	8.94 (1.66)	8.23 (1.57)
Mean diurnal range (°C)	10.33 (0.62)	10.18 (0.74)	10.49 (0.54)	10.48 (0.39)
Temperature seasonality (°C)	4.47 (0.44)	4.43 (0.50)	4.66 (0.33)	4.44 (0.32)
Maximum temperature of warmest month (°C)	19.55 (3.16)	18.32 (3.34)	21.11 (2.20)	20.00 (2.09)
Minimum temperature of coldest month (°C)	− 2.65 (2.19)	− 3.74 (2.19)	− 1.75 (1.88)	− 2.14 (1.58)
Temperature annual range (°C)	22.21 (1.75)	22.08 (1.97)	22.86 (1.38)	22.14 (1.24)
Mean temperature of warmest quarter (°C)	13.20 (2.83)	12.12 (3.01)	14.63 (1.94)	13.56 (1.89)
Mean temperature of coldest quarter (°C)	− 2.65 (2.19)	0.83 (2.17)	2.81 (1.59)	2.31 (1.42)
Mean temperature of driest quarter (°C)	9.81 (3.71)	10.33 (3.32)	11.65 (3.31)	8.16 (3.11)
Isothermality (%)	46.11 (1.52)	45.71 (11.36)	45.44 (1.17)	46.93 (1.43)
Mean temperature of wettest quarter (°C)	5.67 (2.94)	5.71 (3.20)	5.57 (2.35)	6.08 (3.08)
Precipitation				
Annual precipitation (mm year^{-1})	245.91 (181.37)	273.08 (149.54)	195.18 (35.90)	191.22 (28.50)
Precipitation of wettest month (mm year^{-1})	30.15 (18.89)	34.61 (15.31)	24.84 (4.74)	23.03 (3.86)
Precipitation seasonality (%)	24.41 (6.56)	26.99 (7.24)	25.94 (6.14)	21.40 (4.05)
Precipitation of wettest quarter (mm year^{-1})	79.81(53.23)	90.01(45.47)	66.11(14.18)	61.12(12.43)
Precipitation of coldest quarter (mm year^{-1})	67.33 (46.02)	75.06 (40.06)	56.96 (14.20)	50.89 (11.89)
Precipitation of driest month (mm year^{-1})	13.60 (12.51)	14.51 (10.46)	10.31 (2.47)	10.64 (1.82)
Precipitation of driest quarter (mm year^{-1})	46.37 (41.06)	50.14 (32.75)	35.22 (7.21)	35.87 (5.32)
Precipitation of warmest quarter (mm year^{-1})	53.61 (42.91)	54.01 (35.30)	39.82 (10.62)	48.64 (9.68)
Global potential evapo-transpiration (mm year^{-1})	807.87 (101.56)	770.03 (107.48)	856.92 (72.73)	821.49 (69.90)
Global aridity index	0.32 (0.35)	0.38 (0.27)	0.22 (0.05)	0.23 (0.04)
Topography				
Elevation (m.a.s.l.)	468.82 (383.84)	744.99 (357.72)	369.45 (218.20)	216.85 (122.64)
Slope (°)	5.00 (5.76)	6.21 (6.41)	4.16 (3.63)	3.27 (2.73)

Table 2 Potential biodiversity map of darkling beetles classified as percentage (low, medium or high potential) and their occurrence in the different landscape and land-use variables: (i) ecological areas (Oliva et al. 2004), (ii) soil organic carbon stock (kg m^{-2}) (Peri et al. 2018), (iii) sheep density (sheep ha^{-1}) (Pedrana et al. 2011), and (iv) desertification (Del Valle et al. 1998)

Type	Variables	Total area (%)	Low (%)	Medium (%)	High (%)
Ecological areas	Dry steppe	68	29	44	28
	Humid steppe	8	30	11	58
	Shrublands	12	5	14	81
	Forests and alpine vegetation	4	100	0	0
	Sub-Andean grasslands	8	86	13	1
Soil organic carbon (kg m^{-2})	< 4.5	32	44	46	10
	4.5–5.5	34	21	37	42
	> 5.5	34	36	17	47
Sheep density (sheep ha^{-1})	< 0.3	30	59	32	9
	0.3–0.6	35	30	43	27
	> 0.6	35	14	25	61
Desertification	Slightly	9	79	12	9
	Moderately	51	33	31	36
	Severely	40	24	41	35

Discussion

Potential habitat suitability maps

Habitat suitability maps had been used with different objectives, such as studied of auto-ecology of the species (Buse et al. 2007), the impact of climate change (Homburg et al. 2014), and for planning new conservation strategies (Bosso et al. 2018). Most of these studies were conducted with well-known species using large available databases (e.g. large mammals) or for endangered species (e.g. huemul at Patagonia) (Rodríguez et al. 2007; Rosas et al. 2017). However, the use in other groups (e.g. insects) also may be useful to improve the conservation strategies or to predict changes in their distribution due to changes in the landscape (Samways 2007). The employment of these tools was possible due to a recent software development, especially those that predict the PHS using presence data (Guisan and Zimmermann 2000; Soberón and Peterson 2005) in remote areas with low information (Hirzel et al. 2006). However, the modelling can generate spatial auto-correlation errors due to an oversampled in accessible areas (Veloz 2009; Phillips et al. 2009). Some tools avoid these biases, using special software tools (e.g. spatial filter) (Veloz 2009) or checking if human related variables (e.g. distance to localities and routes) presented a strong spatial auto-correlation (Phillips et al. 2009). In our study, human related variables did not greatly influence our models (e.g. eigenvalues were not significant). Beside this, the implementation of filters for data removal (e.g. according closeness of cities and routes) is not possible in areas with low available data (e.g. less than 20 observations per species), as in Southern Patagonia. Another chance is to evaluate the models using other statistics. For example, Biomapper software employs two simple indexes (AVI and CVI) for presence data. Moreover, it is possible to evaluate a model even when the species dataset is small, as it ensures an optimal use of the data to calibrate and evaluate the model (Hirzel et al. 2006). This was one of the main reasons to model PHS using ENFA in several studies around the world (Hirzel et al. 2002), as well as in Patagonia (Martínez Pastur et al. 2016; Rosas et al. 2017, 2018).

ENFA follows the concept of the ecological niche (Grinnell 1917), which links the fitness of individuals to the environment (Hirzel and Le Lay 2008). It is necessary to consider the over-fitting in the modelling to understand how reliable the results are, according to: (i) number of predictor variables included in the models (Munguía et al. 2008) (e.g. we finally included few variables of different types, see Appendix 2), and (ii) the high correlation among the climate (e.g. Worldclim databases) and topographic variables (e.g. in our modelling mean temperature of coldest month and elevation). For those studied species with restricted geographical distribution and high overfitting (Munguía et al. 2008), errors can remain constant when modelling procedures used the same variables for several species (e.g. in our study we modelled ten species using the same predictor variables) (Munguía et al. 2008; Breitman et al. 2015; Rosas et al. 2018). Our PHS models were fitted with a limited database, where the number of localities varied between 14 and 46. However, the model performance according to the validation was not related to the number of available data, e.g. the less accurate models corresponded to *N. sallei* with 25 localities.

In our study, PHS models showed the highest values in the East, North-East and South (arid and semiarid environments) corresponding to typical habitats of darkling beetles belonging to Pimeliinae and some Tenebrionae (Doyen 1994; Matthews et al. 2010). In different studies of Patagonian steppe, tribes Nyctellini, Praocini and Scotobiini represented 82% and 98% of the epigeous species (Sackmann and Flores 2009; Carrara and Flores 2013). Carrara and Flores (2015) indicated that more than 78% of the Patagonian darkling beetles belong to tribes that are distributed in these types of environments around the World. In fact, Patagonian steppe is considered as a special area with high endemism of darkling beetles (Domínguez et al. 2006; Carrara and Flores 2013). Species of Tenebrionidae display a high morphological, physiological, behaviour adaptations and ecological plasticity for desert areas (Cloudsley-Thompson 2001; Matthews et al. 2010). These adaptations allow to the species to live in a wide range of environmental conditions close to their limits of tolerance (Sackmann and Flores 2009). These particularities are reflected in our model outputs, where nine species presented low specialization values (see Fig. 2). However, some species with high potential habitat in the Eastern region showed low marginality values (*N. darwini*, *N. sallei*, *E. lata* and *M. araneiformis*), which indicated that these species avoid the extreme environments of mountain areas (e.g. prefer temperate areas close to the sea). The species with higher potential habitat in the Southern areas showed higher marginality (*E. multipunctata*, *P. bicarinata*, *E. tricostata*, *N. bremi* and *N. corrugata*), indicating a greater preference for extreme environmental conditions (e.g. greater occurrence in areas with low temperature during the coldest month). Finally, *N. fitzroyi* presented higher values of marginality and specialization, which indicated that live in extreme and in a narrow range of environmental conditions (Fig. 3). There are only few studies about phylogenetic, morphological and habitat description of this endemic species (Flores 1997, 1998, 1999; Flores and Vidal 2001), e.g. *Nyctelia* and *Epipedonota* genera present diurnal and crepuscular habits and mainly occurred in valleys and cliffs, while *Mitragenius* genus present nocturnal habits and during the day look for shelter under stones and other vegetal materials.

Environmental characterization of the map of potential biodiversity

PHS-based studies have traditionally addressed the niche issues of single species, and few studies addressed issues of species assemblage (Hirzel and Le Lay 2008; Martínez Pastur et al. 2016; Rosas et al. 2018). In this study, we combined 10 PHS of endemic darkling beetle species to characterize their potential biodiversity in Southern Patagonia. Domínguez et al. (2006) indicated a greater endemism in the South, and Carrara and Flores (2013) identified five areas with high endemism in the East and three in the West near to water bodies in the mountains. This was coincident with our modelling, that identified these areas as higher potential biodiversity (see Fig. 4). It is possible that the higher biodiversity in areas close to water bodies can be related with speciation processes (diversification of new species) due to the isolation during historical periods of drought (Roig-Juñent et al. 2008; Carrara and Flores 2013).

In our modelling, climatic and topographic variables had influenced MPB, where medium and high qualities increased with temperature and decreased with rainfall (see Table 1). Temperature influences their activity patterns, microhabitat preferences and seasonal community composition (Bartholomew and Moghrabi 2018). In addition, darkling beetles presented different behaviour adaptations (e.g. avoid excessive heat during the day) to regulate water loss in arid conditions (Cloudsley-Thompson 2001). Similarly, in Southern Patagonia, Ruggiero et al. (2009) reported a positive relationship between beetle abundance and the increase of minimum daily temperature, while Carrara et al. (2011a) cited a negative relationship between endemic richness distribution and rainfall. Mazia et al. (2006) also found that tenebrionid activity decreased when frequency of daily maximum soil temperature increased. In reference to these adaptations, precipitation dynamics over a geological time in the Patagonian steppe have led to processes of speciation and extinction, leading to the current patterns of distribution and richness of darkling beetles (Carrara and Flores 2013).

Vegetation (NDVI) and soil qualities also influenced MPB of darkling beetles, where the highest qualities were associated to humid steppe and shrublands related to higher SOC stocks. Several studies have found higher beetle activity, biomass and diversity in heterogeneous habitats, e.g. shrub vegetated habitats or landscapes with vegetation patches (e.g. savannah) (Mazia et al. 2006; Liu et al. 2012; Reinhard et al. 2019). Ruggiero et al. (2009) found that shrub cover positively affect beetle abundance in the steppe but negatively in the forests. The reason for complex vegetation preference can be due to favourable temperatures, reducing the risk of desiccation, predation risk, food availability and animal burrows (Liu et al. 2012). Beetle richness also can be related to soil qualities and vegetation, due to these variables affect the food availability and their reproduction success (Mazia et al. 2006; Carrara et al. 2011b; Lescano et al. 2017). Nevertheless, Bartholomew and Moghrabi (2018) found that darkling beetles prefer shrubs due to protection from extreme temperatures instead of predation refuge or food resource.

Trade-offs of desertification and land use with the potential biodiversity

In arid ecosystems, beetles play key functional roles in different processes: (i) biological control, (ii) seed dispersal, (iii) structure of soils, nutrient cycling, and decomposition of organic material, and (iv) serving as food source for birds and mammals (Samways 2007; Cheli et al. 2009; Superina et al. 2009; Aballay et al. 2016). Darkling beetles can be considered as environmental bio-indicators because their abundance and richness (Kaltsas et al. 2012) are sensitive to land-use changes (Newbold et al. 2014). Alterations in vegetation and soil conditions due to management intensity (e.g. livestock) can affect their abundance, diversity, and community composition (Samways 2007; Newbold et al. 2014; Liu et al. 2016; Li et al. 2018). In our study, sheep density and desertification processes had similarities with MPB, where high sheep density (> 0.6 sheep ha^{-1}) and severe desertification occurred in high MPB areas. Nevertheless, darkling beetles can differently respond to lands-use changes (Liu et al. 2016), because their differences in trophic positions and ecological requirements (Homburg et al. 2014). Kaltsas et al. (2012) found temporal changes in density and community composition of beetles when structural vegetation changed due to livestock. The influence of livestock suggest that some groups (e.g. macro-arthropods) are more sensitive to grazing than others, and many groups decline when grazing intensity increased. Newbold et al. (2014) found higher richness and abundance of some species within the long-term grazing closures, but some species tend to increase with grazing. In addition, Reinhard et al. (2019) found that richness and diversity were unaffected in areas with current grazing before another impact (e.g. fire) in the short-term. In Patagonian steppe, grazing and desertification threat biodiversity (Del Valle et al. 1998; Peri et al. 2013, 2016), because affect the vegetation structure and homogenise the landscape affecting species survival (Kaltsas et al. 2012; Lescano et al. 2017; Reinhard et al. 2019). The influence of livestock on vegetation structure due to over-graze lead to desertification in the Patagonian steppe during the last decades (Del Valle et al. 1998; Peri et al. 2013, 2016, 2018). In our study, the best places for grazing and the most affected areas for desertification (see Fig. 1) were coincident with the highest potential biodiversity for darkling beetles. This generates potential trade-offs between the studied factors and its conservation status.

Management and conservation recommendations

Management and conservation strategies must be developed for darkling beetles due to their high endemicity, extinction risk, and their sensitiveness to land use changes (Carrara et al. 2011b; Newbold et al. 2014). Only about 10% of all insects have a scientific name, and the social perception is that insects are insignificant receiving low attention (Samways 2007). However, beetles are amongst the most popular insects for collectors and hobbyist, and some beetles are decidedly charismatic and have been promoted widely in conservation (Buse et al. 2007; Bosso et al. 2018). As it was mentioned before, darkling beetles have a major role in several ecological processes (Cheli et al. 2009; Superina et al. 2009; Aballay et al. 2016), and they are sensitive to land-use changes (Lescano et al. 2017; Li et al. 2018). For this, it is important to include this species group into management and conservation strategies to guarantee their subsistence. One strategy is to identify areas with endemism or greater species richness (Carrara et al. 2011a; Carrara and Flores 2015), and define a special protection status (Carrara et al. 2011b; Carrara and Flores 2013) or propose a differential management (e.g. reduce sheep density). The other strategy is modelling the habitat suitability of the species to known its potential distribution and their environmental requirements to analyse the effective conservation of natural reserves, e.g. this strategy was used in the framework of Natura 2000 (Buse et al. 2007; Bosso et al. 2018). With the modelling is possible to identify potential areas of better habitability for more species (e.g. MPB with the highest values) to re-define networks of natural reserves. From the present study, we determined that only 24.6% of the protected areas in the region corresponded to medium–high MPB qualities, where provincial reserves protect more than national parks. To improve this conservation strategy, it is essential to include transition areas (e.g. farmlands), or new potential habitats due to climate change (Carrara and Flores 2013; Homburg et al. 2014; Bosso et al. 2018). In this sense, our map becomes an useful tool to select areas for future conservation. Samways (2007) proposed three categories for insect conservation strategies: (i) reserve selection, (ii) conservancy, that represents areas adjacent to reserves increasing their habitat and chances of long-term survival, and (iii) land-sparing. The land-sparing can be an interesting strategy by including ranches with greater sheep density and high MPB values (e.g. reduce the shrub removal or establish some retention patches without grazing). Some studies suggested that modifications of traditional grazing practices (e.g. intensity, patchiness, and seasonality of grazing) can be used to increase spatial and temporal heterogeneity in vegetation at the landscape scale, and improve habitat quality for species of conservation concern (Newbold et al. 2014).

Conclusions

PHS models allowed us to increase the knowledge about auto-ecology and potential distribution of the studied species, as well as to define the relationships among the darkling beetles and its environmental requirements (e.g. specialization and marginality). The development of a MPB allowed simplifying the information for the different species, generating a powerful tool for decision-making. This map can be used for: (i) support ecological, biogeographic and local studies of endemic darkling beetles, (ii) identify potential trade-off between economic activities (e.g. livestock) and conservation, and (iii) understand the potential risks of desertification processes or climate change. These results also can contribute to define new management planning at landscape level, or to propose new alternatives for biodiversity conservation based on less studied species, as the darkling beetles.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Research involving human and animal participants This research not involve human and animal participants.

References

Aballay FH, Flores GE, Silvestro VA, Zanetti NI, Centeno ND (2016) An illustrated key to and diagnoses of the species of Tenebrionidae (Coleoptera) associated with decaying carcasses in Argentina. Ann Zool 66:703–726. https://doi.org/10.3161/00034541ANZ2016.66.4.021

Bartholomew A, Moghrabi J (2018) Seasonal preference of darkling beetles (Tenebrionidae) for shrub vegetation due to high temperatures, not predation or food availability. J Arid Environ 156:34–40. https://doi.org/10.1016/j.jaridenv.2018.04.008

Bosso L, Smeraldo S, Rapuzzi P, Sama G, Garonna AP, Russo D (2018) Nature protection areas of Europe are insufficient to preserve the threatened beetle *Rosalia alpina* (Coleoptera: Cerambycidae): evidence from species distribution models and conservation gap analysis. Ecol Entomol 43:192–203. https://doi.org/10.1111/een.12485

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow F (2002) Evaluating resource selection functions. Ecol Model 157:281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Breitman MF, Bonino MF, Sites JW Jr, Avila LJ, Morando M (2015) Morphological variation, niche divergence, and phylogeography of lizards of the *Liolaemus lineomaculatus* section (Liolaemini) from Southern Patagonia. Herpetol Monogr 29:65–88. https://doi.org/10.1655/HERPMONOGRAPHS-D-14-00003

Buse J, Schröder B, Assmann T (2007) Modelling habitat and spatial distribution of an endangered longhorn beetle a case study for saproxylic insect conservation. Biol Conserv 137:372–381. https://doi.org/10.1016/j.biocon.2007.02.025

Carrara R, Flores GE (2013) Endemic tenebrionids (Coleoptera: Tenebrionidae) from the Patagonian steppe: a preliminary identification of areas of micro-endemism and richness hotspots. Entomol Sci 1:100–111. https://doi.org/10.1111/j.1479-8298.2012.00542.x

Carrara R, Flores GE (2015) Endemic epigean Tenebrionids (Coleoptera: Tenebrionidae) from the Andean Region: exploring the Patagonian-diversification hypothesis. Zootaxa 4007:47–62. https://doi.org/10.11646/zootaxa.4007.1.3

Carrara R, Vázquez DP, Flores GE (2011a) Habitat specificity can blur the predictions of species–energy theory: a case study of tenebrionid beetles adapted to aridity. J Arid Environ 75:703–710. https://doi.org/10.1016/j.jaridenv.2010.11.007

Carrara R, Cheli GH, Flores GE (2011b) Biogeographic patterns of epigean tenebrionids (Coleoptera: Tenebrionidae) from Protected Natural Area Peninsula Valdes, Argentina: implications for its conservation. Rev Mex Biodivers 82:1297–1310

Cheli GH, Corley J, Castillo LD, Martínez F (2009) Una aproximación experimental a la preferencia alimentaria de *Nyctelia circumundata* (Coleoptera: Tenebrionidae) en el Noreste de la Patagonia. Interciencia 34:771–776

Cloudsley-Thompson J (2001) Thermal and water relations of desert beetles. Naturwissenschaften 88:447–460. https://doi.org/10.1007/s001140100256

Del Valle HF, Elissalde NO, Gagliardini DA, Milovich J (1998) Status of desertification in the Patagonian region: assessment and mapping from satellite imagery. Arid Land Res Manag 12:95–121. https://doi.org/10.1080/15324989809381502

Domínguez CM, Roig-Juñent S, Tassin JJ, Ocampo FC, Flores GE (2006) Areas of endemism of the Patagonian steppe: an approach based on insect distributional patterns using endemicity analysis. J Biogeogr 33:1527–1537. https://doi.org/10.1111/j.1365-2699.2006.01550.x

Doyen JT (1994) Cladistic relationships among Pimeliinae Tenebrionidae (Coleoptera). J NY Entomol Soc 101:443–514

Elith J, Leathwick J (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

ESRI (2011) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Inc., Redlands

Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimada J, Umland J, Werner M, Oskin M, Burbank D, Alsdorf D (2007) The shuttle radar topography mission. Rev Geophys 45:RG2004. https://doi.org/10.1029/2005RG000183

Flores GE (1997) Revisión de la tribu Nycteliini (Coleoptera: Tenebrionidae). Rev Soc Entomol Argent 56:1–19

Flores GE (1998) Tenebrionidae. In: Morrone JJ, Coscarón S (eds) Biodiversidad de artrópodos argentinos: Una perspectiva biotaxonómica. Ediciones Sur, La Plata, pp 232–240

Flores GE (1999) Systematic revision and cladistic analysis of the Neotropical genera Mitragenius Solier, Auladera Solier and Patagonogenius gen. n. (Coleoptera: Tenebrionidae). Insect Syst Evol 30:361–396. https://doi.org/10.1163/187631200X00516

Flores GE, Vidal P (2001) Systematic revision and redefinition of the Neotropical genus Epipedonota Solier (Coleoptera: Tenebrionidae), with descriptions of eight new species. Insect Syst Evol 32:1–43. https://doi.org/10.1163/187631201X00010

Grinnell J (1917) Field tests of theories concerning distributional control. Am Nat 51:115–128. https://doi.org/10.1086/279591

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Hirzel AH, Arlettaz R (2003) Modelling habitat suitability for complex species distributions by the environmental-distance geometric mean. Environ Manag 32:614–623. https://doi.org/10.1007/s00267-003-0040-3

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. J Appl Ecol 45:1372–1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x

Hirzel AH, Helfer V, Metral F (2001) Assessing habitat-suitability models with a virtual species. Ecol Model 145:111–121. https://doi.org/10.1016/S0304-3800(01)00396-9

Hirzel AH, Hausser J, Chessel D, Perrin N (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology 83:2027–2036. https://doi.org/10.1890/0012-9658(2002)083%5b2027:ENFAHT%5d2.0.CO;2

Hirzel AH, Hausser J, Perrin N (2004) Biomapper 3,1. Division of Conservation Biology, University of Bern, Bern

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating habitat suitability models with presence-only data. Ecol Model 199:142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017

Homburg K, Brandt P, Drees C, Assmann T (2014) Evolutionarily significant units in a flightless ground beetle show different climate niches and high extinction risk due to climate change. J Insect Conserv 18:781–790. https://doi.org/10.1007/s10841-014-9685-x

Kaltsas D, Trichas A, Mylonas M (2012) Temporal organization patterns of epigean beetle communities (Coleoptera: *Carabidae*, *Tenebrionidae*) in different successional stages of eastern Mediterranean maquis. J Nat Hist 46:495–515. https://doi.org/10.1080/00222933.2011.645897

Lescano MN, Elizalde L, Werenkraut V, Pirk GI, Flores GE (2017) Ant and tenebrionid beetle assemblages in arid lands: their associations with vegetation types in the Patagonian steppe. J Arid Environ 138:51–57. https://doi.org/10.1016/j.jaridenv.2016.12.002

Li FR, Liu JL, Ren W, Liu LL (2018) Land-use change alters patterns of soil biodiversity in arid lands of northwestern China. Plant Soil 428:1–18. https://doi.org/10.1007/s11104-018-3673-y

Lillesand TM, Kiefer RW (2000) Remote sensing and image interpretation, 4th edn. Wiley, New York

Liu J, Li F, Liu C, Liu Q (2012) Influences of shrub vegetation on distribution and diversity of a ground beetle community in a Gobi Desert ecosystem. Biodivers Conserv 21:2601–2619. https://doi.org/10.1007/s10531-012-0320-4

Liu R, Zhu F, Steinberger Y (2016) Changes in ground-dwelling arthropod diversity related to the proximity of shrub cover in a desertified system. J Arid Environ 124:172–179. https://doi.org/10.1016/j.jaridenv.2015.08.014

Martínez Pastur G, Peri PL, Soler R, Schindler S, Lencinas MV (2016) Biodiversity potential of *Nothofagus* forests in Tierra del Fuego (Argentina): tool proposal for regional conservation planning. Biodivers Conserv 25:1843–1862. https://doi.org/10.1007/s10531-016-1162-2

Matthews EG, Lawrence JF, Bouchard P, Steiner WE, Ślipiński SA (2010) Tenebrionidae Latreille (1802). In: Leschen RAB, Beutel RG, Lawrence JF (eds) Handbook of zoology. Coleoptera, Beetles. Morphology and systematics (Elateroidea, Bostrichiformia partim), vol 2. De Gruyter, Berlin, pp 574–659

Mazia C, Chaneton E, Kitzberger T (2006) Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. J Arid Environ 67:177–194. https://doi.org/10.1016/j.jaridenv.2006.02.006

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst

Munguía M, Townsend Peterson A, Sánchez-Cordero V (2008) Dispersal limitation and geographical distributions of mammal species. J Biogeogr 35:1879–1887. https://doi.org/10.1111/j.1365-2699.2008.01921.x

Newbold TS, Stapp P, Levensailor KE, Derner JD, Lauenroth WK (2014) Community responses of arthropods to a range of traditional and manipulated grazing in shortgrass steppe. Ecol Entomol 43:556–568. https://doi.org/10.1603/EN12333

Oliva G, Gonzalez L, Ruial P (2004) Áreas Ecológicas. In: Gonzalez L, Rial P (eds) Guía Geográfica Interactiva de Santa Cruz. INTA, Buenos Aires, pp 14–15

ORNL DAAC (2008) MODIS Collection 5 land products global subsetting and visualization tool. ORNL DAAC, Oak Ridge

Pedrana J, Bustamante J, Rodriguez A, Travaini A (2011) Primary productivity and anthropogenic disturbance as determinants of Upland Goose *Chloephaga picta* distribution in Southern Patagonia. IBIS 153:517–530. https://doi.org/10.1111/j.1474-919X.2011.01127.x

Peri PL, Lencinas MV, Martínez Pastur G, Wardell-Johnson GW, Lasagno R (2013) Diversity patterns in the steppe of Argentinean Southern Patagonia: environmental drivers and impact of grazing. In: Morales MB, Traba Diaz J (eds) Steppe ecosystems: biological diversity, management and restoration. Nova Science Publishers, Inc., Madrid, pp 73–96

Peri PL, Lencinas MV, Bousson J, Lasagno R, Soler R, Bahamonde H, Martinez Pastur G (2016) Biodiversity and ecological long-term plots in Southern Patagonia to support sustainable land management: the case of PEBANPA Network. J Nat Conserv 34:51–64. https://doi.org/10.1016/j.jnc.2016.09.003

Peri PL, Rosas YM, Ladd B, Toledo S, Lasagno RG, Martínez Pastur G (2018) Modelling soil carbon content in South Patagonia and evaluating changes according to climate, vegetation, desertification and grazing. Sustainability 10:438. https://doi.org/10.3390/su10020438

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol Appl 19:181–197. https://doi.org/10.1890/07-2153.1

Reinhard JE, Geissler K, Blaum N (2019) Short-term responses of darkling beetles (Coleoptera: Tenebrionidae) to the effects of fire and grazing in savannah rangeland. Insect Conserv Divers 12:39–48. https://doi.org/10.1111/icad.12324

Rodríguez JP, Brotons L, Bustamante J, Seoane J (2007) The application of predictive modelling of species distribution to biodiversity conservation. Divers Distrib 13:243–251. https://doi.org/10.1111/j.1472-4642.2007.00356.x

Roig-Juñent SA, Agrain F, Carrara R, Ruiz-Manzanos E, Tognelli MF (2008) Description and phylogenetic relationships of two new species of *Baripus* (Coleoptera: Carabidae: Broscini) and considerations regarding patterns of speciation. Ann Carnegie Mus 77:211–227. https://doi.org/10.2992/0097-4463-77.1.211

Rosas YM, Peri PL, Herrera AH, Pastore H, Martínez Pastur G (2017) Modeling of potential habitat suitability of *Hippocamelus bisulcus*: effectiveness of a protected areas network in Southern Patagonia. Ecol Process 6:28. https://doi.org/10.1186/s13717-017-0096-2

Rosas YM, Peri PL, Martínez Pastur G (2018) Potential biodiversity map of lizard species in Southern Patagonia: environmental characterization, desertification influence and analyses of protection areas. Amphib Reptil 39:289–301. https://doi.org/10.1163/15685381-20181001

Ruggiero A, Sackmann P, Farji-Brener AG, Kun M (2009) Beetle abundance–environment relationships at the Subantarctic–Patagonian transition zone. Insect Conserv Divers 2:81–92. https://doi.org/10.1111/j.1752-4598.2009.00045.x

Sackmann P, Flores GE (2009) Temporal and spatial patterns of tenebrionid beetle diversity in NW Patagonia, Argentina. J Arid Environ 73:1095–1102. https://doi.org/10.1016/j.jaridenv.2009.05.007

Samways MJ (2007) Insect conservation: a synthetic management approach. Annu Rev Entomol 52:465–487. https://doi.org/10.1146/annurev.ento.52.110405.091317

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distribution areas. Biodivers Inform 2:1–10. https://doi.org/10.17161/bi.v2i0.4

Superina M, Fernández Campón F, Stevani EL, Carrara R (2009) Summer diet of the pichi *Zaedyus pichiy* (Xenarthra: Dasypodidae) in Mendoza Province, Argentina. J Arid Environ 73:683–686

Tognelli MF, Roig Juñent S, Marvaldi AE, Flores GE, Lobo JM (2009) An evaluation of methods for modelling distribution of Patagonian insects. Rev Chil Hist Nat 82:347–360

Veloz SD (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. J Biogeogr 36:2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Zhao M, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 329:940–943. https://doi.org/10.1126/science.1192666

Zomer RJ, Trabucco A, Bossio DA, Van Straaten O, Verchot LV (2008) Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agric Ecosyst Environ 126:67–80. https://doi.org/10.1016/j.agee.2008.01.014