J Insect Conserv (2015) 19:33–43
DOI 10.1007/s10841-014-9740-7

ORIGINAL PAPER

Species conservation under future climate change: the case of *Bombus bellicosus*, a potentially threatened South American bumblebee species

Aline C. Martins · Daniel P. Silva · Paulo De Marco Jr. · Gabriel A. R. Melo

Received: 26 June 2014 / Accepted: 21 November 2014 / Published online: 29 November 2014

Abstract Bees ensure 35 % of global food production, but this service is endangered due to several threats. Declines in bumblebee populations (genus *Bombus*) have been reported worldwide. *Bombus bellicosus* is one of the rare cases of reported threatened bumblebees in South America. It was once widespread in southern Brazil's grasslands until the 1960s. During that time, that area underwent increasing land use which led to a decrease in bee abundance and richness, and to local disappearance of *B. bellicosus*. Climate change is also believed to cause declines in the abundance of *B. bellicosus*. Here we used species distribution models to assess potential effects of climate changes on the distribution of *B. bellicosus* in southern Brazil, considering both current and future climate scenarios. Our results show that the suitable climatic conditions for *B. bellicosus* will retreat southwards. A wax cover inside its nests is usually related to *Bombus* species inhabiting cooler climates. This cover enables the maintenance of higher temperatures inside the nest and may be deleterious for the species under future warmer climates. Continuously growing land use is the second major threat to this pollinator. The results presented here may eventually provide theoretical grounds and enable practical conservation actions for *B. bellicosus* protection in South America, especially given the potential adverse effects of climate changes for this species.

Keywords Species distribution modelling · Bumblebee · Pollinator · Climate change · South America · Grasslands

Introduction

Bees are the main group of animal pollinators and ensure at least 35 % of global food production (Klein et al. 2003; Kremen et al. 2007; Klatt et al. 2014). The pollination of crops and wild plants by animals represent one of the ecosystem services that are at risk due to fast and growing anthropogenic changes (Steffan-Dewenter et al. 2005; Biesmeijer et al. 2006; Aizen and Harder 2009; Potts et al. 2010). The main factors determining recent environmental changes and, consequently, bee's decline worldwide, are land use and climate change (Travis 2003; MEA 2005; Tylianakis et al. 2008). Jointly, these factors may cause extinctions, shifts in species ranges, and changes in species' ecological and phenological events (Walther et al. 2002; Parmesan and Yohe 2003; Parmesan 2006; Tylianakis et al. 2008).

Population declines are well documented for honey bees as well as for bumblebees (genus *Bombus*), especially in Europe and North America (Williams and Osborne 2009; Bommarco et al. 2012; Colla et al. 2012; Bartomeus et al.

Electronic supplementary material The online version of this article (doi:10.1007/s10841-014-9740-7) contains supplementary material, which is available to authorized users.

A. C. Martins · G. A. R. Melo
Laboratório de Biologia Comparada de Hymenoptera,
Departamento de Zoologia, Universidade Federal do Paraná,
Caixa Postal 19020, Curitiba, PR CEP 81531-980, Brazil

D. P. Silva (✉)
Instituto de Ciências Biológicas, Universidade Federal do Pará,
Rua Augusto Correia, Guamá, Belém, PA CEP 66075-110,
Brazil
e-mail: daniel.paivasilva@gmail.com

P. De Marco Jr.
Theory, Metapopulation and Landscape Lab, Departamento de
Ecologia, Instituto de Ciências Biológicas, Universidade Federal
de Goiás Campus II, Caixa Postal 131, Goiânia,
GO CEP 74001-970, Brazil

2013). Bumblebees are effective crop pollinators (Garratt et al. 2014) and the main factors responsible for the observed population declines are shortage of food sources and nesting sites due to habitat loss (Goulson et al. 2008). Pesticides (Thompson 2001; Whitehorn et al. 2012) and competition with introduced honeybees (Thomson 2004), or other bumblebee species (Morales et al. 2013), also exert a negative influence in bumblebee populations. A combination of these factors may also be a possible explanation for the observed decreases in *Bombus* abundance (Winfree et al. 2009; Bartomeus et al. 2013). Another reported factor that causes vulnerability in bumblebee populations is the low genetic diversity related to its social behaviour (Chapman and Bourke 2001; Ellis et al. 2006). However, the existence of a relationship between social behaviour traits and observed abundance declines of social insects is still controversial, since for some authors it exists (Winfree et al. 2009) and for others it does not (e.g. Bartomeus et al. 2013), or depends on environmental disturbance affecting the species (Williams et al. 2010).

So far, bumblebee declines in South America have gone unnoticed until *Bombus bellicosus* Smith, 1879 was reported to be locally extinct in the Brazilian state of Paraná, Southern Brazil (Martins and Melo 2009). Also *Bombus dahlbomii* Guérin, 1835 was reported as being replaced by the invasive species *Bombus terrestris* (Linnaeus, 1758) in Chile and Argentina (Morales et al. 2013). *B. bellicosus* is a surface ground-nesting bee, which requires only soil and plant detritus to build its nest (Varela 1992a, b). Females of *B. bellicosus* cover their nest cavity with a wax layer—possibly as a protection against cold temperatures. This is a unique trait among tropical and subtropical *Bombus* that links *B. bellicosus* to temperate and sub-temperate climates (Sakagami et al. 1967a). The original known distribution of *B. bellicosus* ranges from latitude 2446’S in southern Brazil up to Uruguay and northern Argentina (Martins and Melo 2009), always associated with native grasslands (Moure and Sakagami 1962).

Bombus bellicosus was the dominant native bee species in Paraná’s first plateau, southern Brazil, until the 1960s (Sakagami et al. 1967b; Sakagami and Laroca 1971). Since then, this region underwent intense land use by urbanization and/or agriculture, leading to a general local decrease in bee abundance and richness and to disappearance of *B. bellicosus* (Martins and Melo 2009; Martins et al. 2013). Despite the visible effect of intense land use in the past four decades, this species still survives in agricultural patches in more southern regions (Martins and Melo 2009). In Europe, land cover together with climate change influenced both richness and local abundance in bumblebees (Herrera et al. 2014). This leads us to question whether its disappearance in the northern limit of its distribution in southern Brazil was caused only by habitat loss or if climate change may have also played an important role in the species disappearance from its northernmost occurrence limit in Brazil. In South America, range shifts and species losses caused by climate change have been predicted for different groups: Atlantic forest trees (Colombo and Joly 2010), amphibians (Lemes and Loyola 2013), marsupials (Loyola et al. 2012) and moths (Ferro et al. 2014).

However, information on many life-history features of *B. bellicosus* and on effects of environmental changes on its natural habitats (the Hutchinsonian shortfall; Cardoso et al. 2011) are lacking. Such absence of basic biological data regarding *B. bellicosus* occurs in parallel with a lack of broad scale quality data on distribution (the Wallacean shortfall; Whittaker et al. 2005), a knowledge gap observed for many other insect species (Diniz-Filho et al. 2010). The Wallacean shortfall is an undeniable obstacle hindering the assessment of insect species under conservation biogeography frameworks especially when we think of species conservation in broad scales (Whittaker et al. 2005; Diniz-Filho et al. 2010; Cardoso et al. 2011) and is an important motive for continuous field surveys to assess insect species distributions (Diniz-Filho et al. 2010).

A possible alternative to fully consider insect distributions and transcend the Wallacean shortfall in broad-scale studies is to use species distribution modelling (SDMs). Usually, these methods relate modelled occurrences of observed species with environmental variables of the known sampling sites to predict new areas suitable for its occurrence (Guisan and Zimmermann 2000; Kearney 2006). These techniques have been employed before to (1) determine insect species’ distributions and inform suitable areas for future surveys (Silva et al. 2013, 2014), (2) pinpoint modelled species rich areas uncovered by the available protected areas network (Nóbrega and De Marco 2011), and (3) to evaluate the effects of future climate changes on species distributions (Loyola et al. 2012; Lemes and Loyola 2013). Considering this context, we used SDMs to address the potential effects of climate change in distributions of *B. bellicosus* in southern Brazil considering both current and future climate change scenarios.

Materials and methods

Occurrence of *Bombus bellicosus*

We obtained a total of 303 records of *B. bellicosus* occurrence from (1) literature records; (2) the online datasets: *CRIA’s Species Link* (http://splink.cria.org.br), *Global Biodiversity Information Facility* (http://www.gbif.org), *Discover Life Bee Species Guide* (http://www.discover-life.org), World Checklist (Ascher and Pickering

2014); and (3) museum collections (see Supplementary Material). We used Google Earth (Google Inc. 2013) to acquire approximate geographical coordinates from downtown of each city near sites where *B. bellicosus* occurred, when lacking a precise geographical information. We assembled 171 unique occurrences to be used in the modelling procedures (grid cell resolution of 2.5 arc-min ≈ grid-cells with sizes of 0.041° in the tropics; see below). Figure 1 shows the spatial distribution of all unique *B. bellicosus* occurrences we obtained.

We used all occurrences to model the potential distribution of *B. bellicosus*, including the sites mentioned by Martins and Melo (2009), where the species were observed after the early 1980s, for two reasons. At first, as we previously mentioned, Wallacean shortfalls severely affect insect distributional data elsewhere, especially in tropical regions (Diniz-Filho et al. 2010; Kamino et al. 2011). If we were to assume the occurrence records only sampled after 1980 were the most reliable distributional information on the species to infer its distribution (a progressive data quality measure, since *Bombus* queens usually live for less than 1 year; Michener 2007), nearly 80 % of the dated occurrences (~290 out of the total 303) would be missing (Figure S1A). Additionally, much of the species known distribution would be disregarded (Figure S1B). A higher number of occurrences may eventually add just a small amount, or even reduce, models' accuracy (Stockwell and Peterson 2002). Still, we are dealing with a species potentially targeted for conservation purposes, so a higher number of known occurrences will provide a larger amount of areas which may be relevant for estimating its future distribution. The second reason for using all occurrences was that in preliminary tests we carried out, even if we removed the sites where the species is no longer observed, the same areas were still predicted as being suitable for the occurrence of *B. bellicosus*.

Environmental data, principal component variables, and modelling procedures

A summary of all methods of analysis and input data are presented in Fig. 2. For the current scenario, we used the

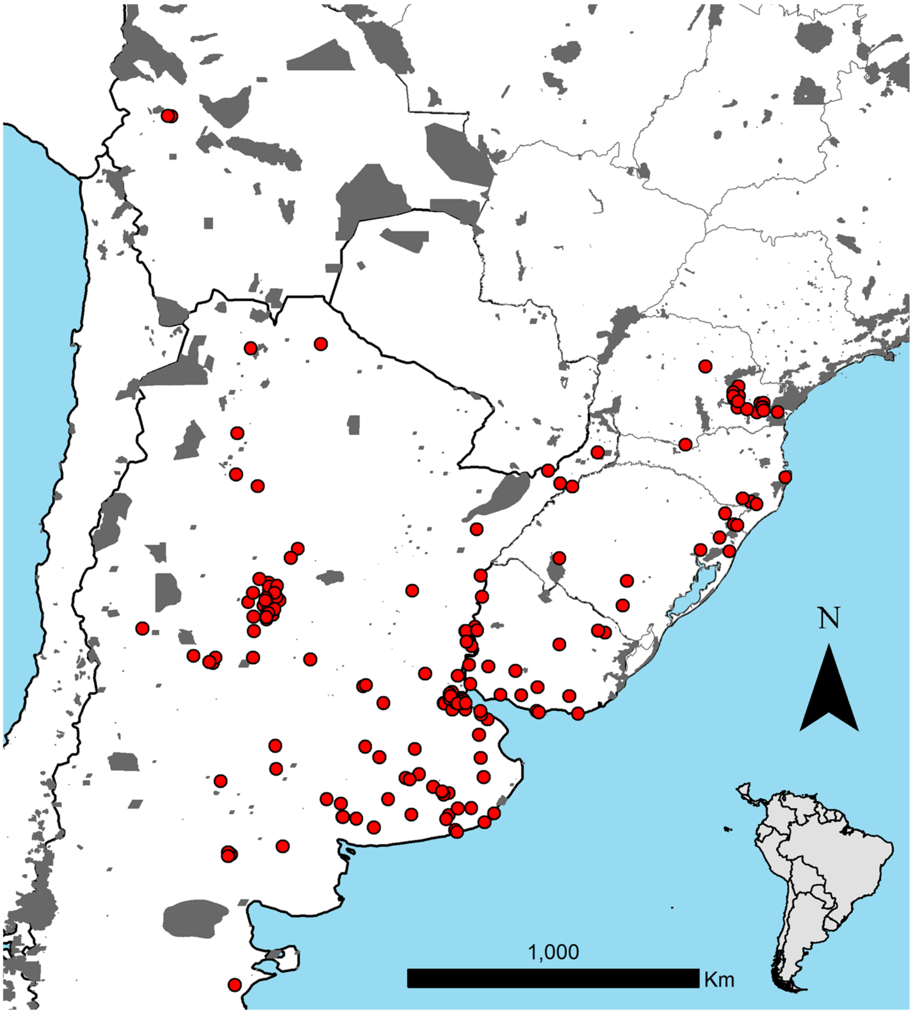

Fig. 1 *Bombus bellicosus* geographical distribution. The map shows the around 170 points of occurrence for *B. bellicosus* in southern South America, sampled from literature and museum collections, which are used as input distribution for all the modelling approaches. *Thick lines* delimit South American countries and *thin lines* delimit provinces or states of each country

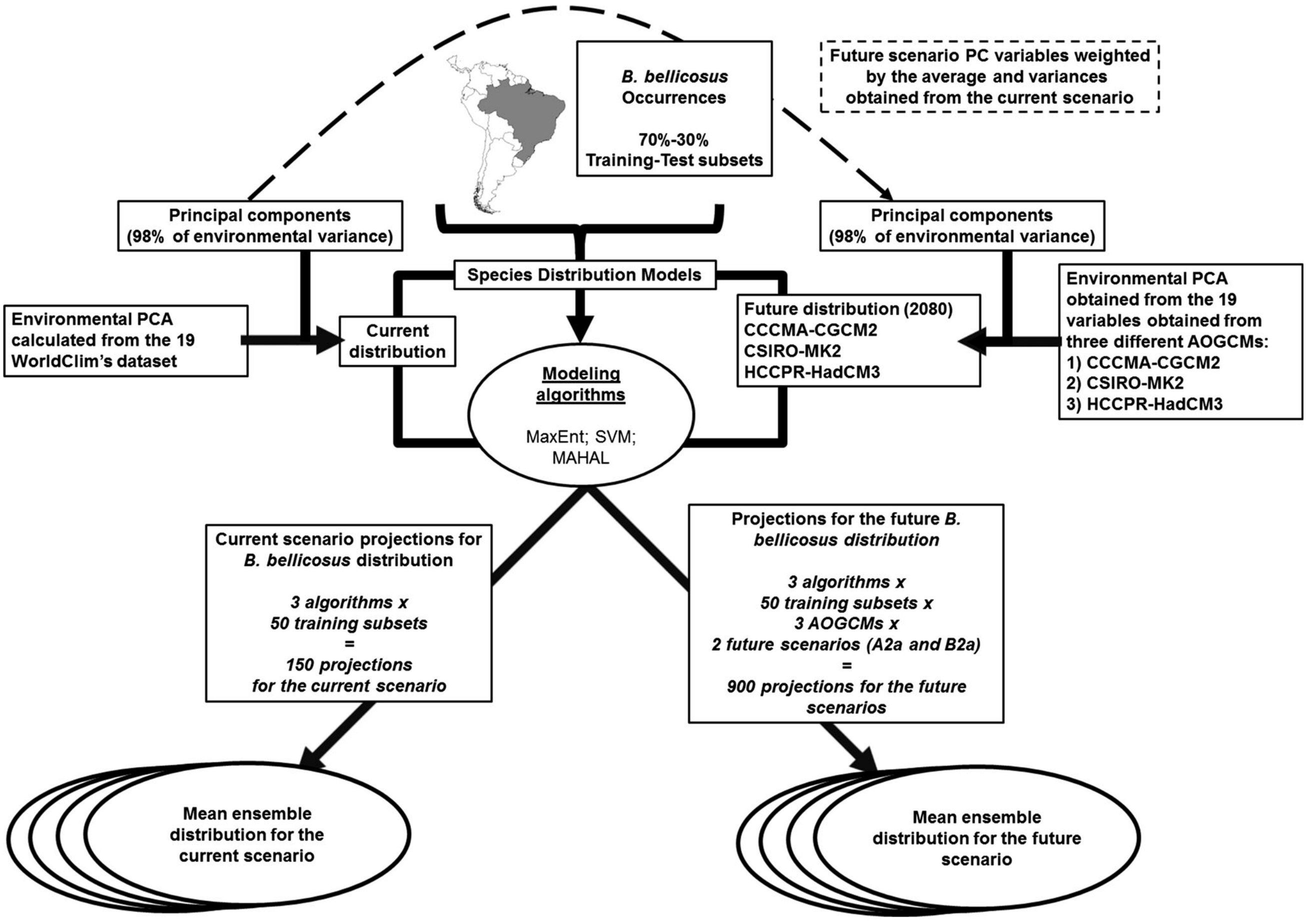

Fig. 2 Flowchart representing stages of analysis in this study. The flowchart represent the stages of analysis, methods employed (algorithms), source of climatic data, and data inputs used in the distribution modelling for *Bombus bellicosus* current and future distribution under climate change

19 environmental variables available from the WorldClim's dataset (http://www.worldclim.org/current, Hijmans et al. 2005). We used a Principal Components Analysis (PCA) on a correlation matrix, to derive 19 principal components (PCs hereon), from which the first seven were used as our final environmental layers (98 % of all original climatic variation; Table S1). We obtained the same 19 variables for the year 2080 for three different Atmosphere–Ocean General Circulation Models (AOGCMs; CCCMA-CGM2, CSIRO-MK2.0, and UKMO-HADCM3) from CIAT (http://ccafs-climate.org) considering both optimistic and pessimistic emission scenarios (B2a and A2a, respectively). Then, we projected the linear combinations of all 19 PCs obtained for the current scenario into each different future AOGCM scenario. We also used the first seven PCs obtained for each future climatic scenario in the modelling procedures to predict the future distribution of *B. bellicosus*. Using PCs to predict species distribution is recommended to reduce collinearity among environmental variables, and to avoid model overfitting, which may result in biologically unreliable species potential distributions (Jiménez-Valverde et al. 2011; Serra et al. 2012; Silva et al. 2014).

Given the uncertainty involved with SDMs (Barry and Elith 2006; Diniz-Filho et al. 2009; Rocchini et al. 2011), we evaluated *B. bellicosus*' distributions using three different modelling algorithms: (1) Maximum Entropy (Phillips et al. 2006; Phillips and Dudik 2008) implemented in Maxent (Phillips et al. 2006); (2) Support Vector Machines (SVM; Schölkopf et al. 2001; Tax and Duin 2004); and (3) Mahalanobis distance (MAHAL; Farber and Kadmon 2003) implemented in open modeller desktop (Muñoz et al. 2011). The later algorithm is simpler and usually needs presence-only data to predict the potential distribution of the targeted species. Meanwhile, Maxent and SVM are artificial intelligence algorithms that are more complex and tend to better predict the known/true distribution of the target species (Rangel and Loyola 2012).

We used 50 subsets of occurrences of *B. bellicosus*, divided into 70 % training and 30 % testing subsets to, respectively, produce the potential distributions and evaluate them, considering the current and all future climatic scenarios. *B. bellicosus* is a potentially targeted species for future practical conservation actions. Thus, we considered the ROC threshold to cut the modelled suitability matrices into presence/absence maps. This threshold balances both omission and commission errors and assures higher prediction rates than other thresholds usually considered in modelling species distribution (Liu et al. 2005; Barbet-Massin et al. 2012). We used true skilled statistics (TSS hereafter; Allouche et al. 2006), a threshold-dependent statistics which varies from −1 to 1, to assess models' performance. Negative or near zero TSS values represent distributions which were not better than a random distribution, while values near one represent a perfect agreement between the observed and the modelled species' distribution in current climatic scenarios (Allouche et al. 2006).

We produced a total of 1,050 distribution maps for *B. bellicosus*, for both current ($n = 150$) and future scenarios ($n = 900$, 450 for each). We used both frequency maps (Araújo and New 2007) and mean ensemble distributions of all 50 potential distributions obtained in each climatic scenario (current, optimistic and pessimistic future climatic conditions) to represent the species' final potential distributions in each combination of algorithm and AOGCM used. Additionally, we also show mean consensus distribution for the species in each one of the three climatic scenarios considered (current, optimistic, and pessimistic future). This ensemble method is considered one of the most reliable to determine the potential distributions of species from different modelling algorithms (Marmion et al. 2009).

Finally, we assessed the IUCN's World Database on the Protected Areas website (http://protectedplanet.net/) to obtain the South American reserve network (categories ranging from I to IV ≈ strict reserves). Then, we overlaid the South American network of protected areas (PA hereon) onto the potential distributions of *B. bellicosus* to evaluate its current and future conservation vulnerability under different future climatic scenarios.

Results

The modelled distributions for *B. bellicosus* had good prediction rates overall. The TSS values generally reached values higher than 0.70 (0.788 ± 0.038; mean ± SD), which indicates a good model fit (MAX 0.798 ± 0.054; MAHAL 0.779 ± 0.023; SVM 0.787 ± 0.028). In the current scenario, regions extending from southern Brazil, Uruguay, and southeastern Paraguay, up to central Argentina were always predicted as suitable for *B. bellicosus* occurrence. This suitability occurred regardless of the inherent uncertainty and variance of both the SDMs and the AOGCM models considered, as shown in the frequency maps and consensual distributions (Fig. 3). The more restricted distribution obtained for the current scenario was mainly determined by the consensual distribution obtained with the SVM algorithm (Fig. 3).

Our resulting distribution of *B. bellicosus* for the future scenarios showed a clear trend despite intrinsic differences of the considered algorithms (AOGCMs, and the emission scenarios): the suitable climatic conditions observed for *B. bellicosus* in the present will retreat southwards, regardless of the climate scenario and algorithm considered (Fig. 3). We observed the same trend in the consensual distributions produced by each combination of modelling algorithm and climatic scenario. According to these combinations, *B. bellicosus* may occupy areas ranging from the southern Brazilian state of Rio Grande do Sul, Uruguay, and central/south Argentina. Nonetheless, we also predicted the occurrence of a disaggregated patch of suitable landscapes for southern Brazilian states (Paraná, Santa Catarina, and Rio Grande do Sul), where grid cells had average altitudes of 675 ± 305 (mean ± SD) meters above sea level, at least for the distributions produced by both Maxent and MAHAL. The models generated for the future distributions with SVM algorithms did not produce such fractioned distribution patch in southern Brazil. When we consider the ensemble distributions, suitable areas for *B. bellicosus* near the Andean ridge may also be observed, although in a smaller frequency for the distributions of *B. bellicosus* produced by the current climatic scenario (Fig. 3). Considering the current, pessimistic and optimistic future potential distributions obtained with all different modelling algorithms, *B. bellicosus* is expected to occur in some of the available South American protected areas (Fig. 4). Nonetheless, southern protected areas may provide better refuges than northern ones in both future and potential climatic scenarios.

Discussion

Climate change may be a key factor for the southward retraction of *B. bellicosus* distribution under future climate change scenarios, as shown by our potential models. The current PA network in South America will be able to protect at least some segments of *B. bellicosus* potential future distributions. Models of future distribution for other bee species also show the loss of suitable areas in future climate change scenarios (Giannini et al. 2012). Climate change in the next 50 years is pointed out as a major factor in forecasts of distribution range changes for Atlantic forest trees (Colombo and Joly 2010), amphibians (Lemes and Loyola 2013) and marsupials (Loyola et al. 2012). For

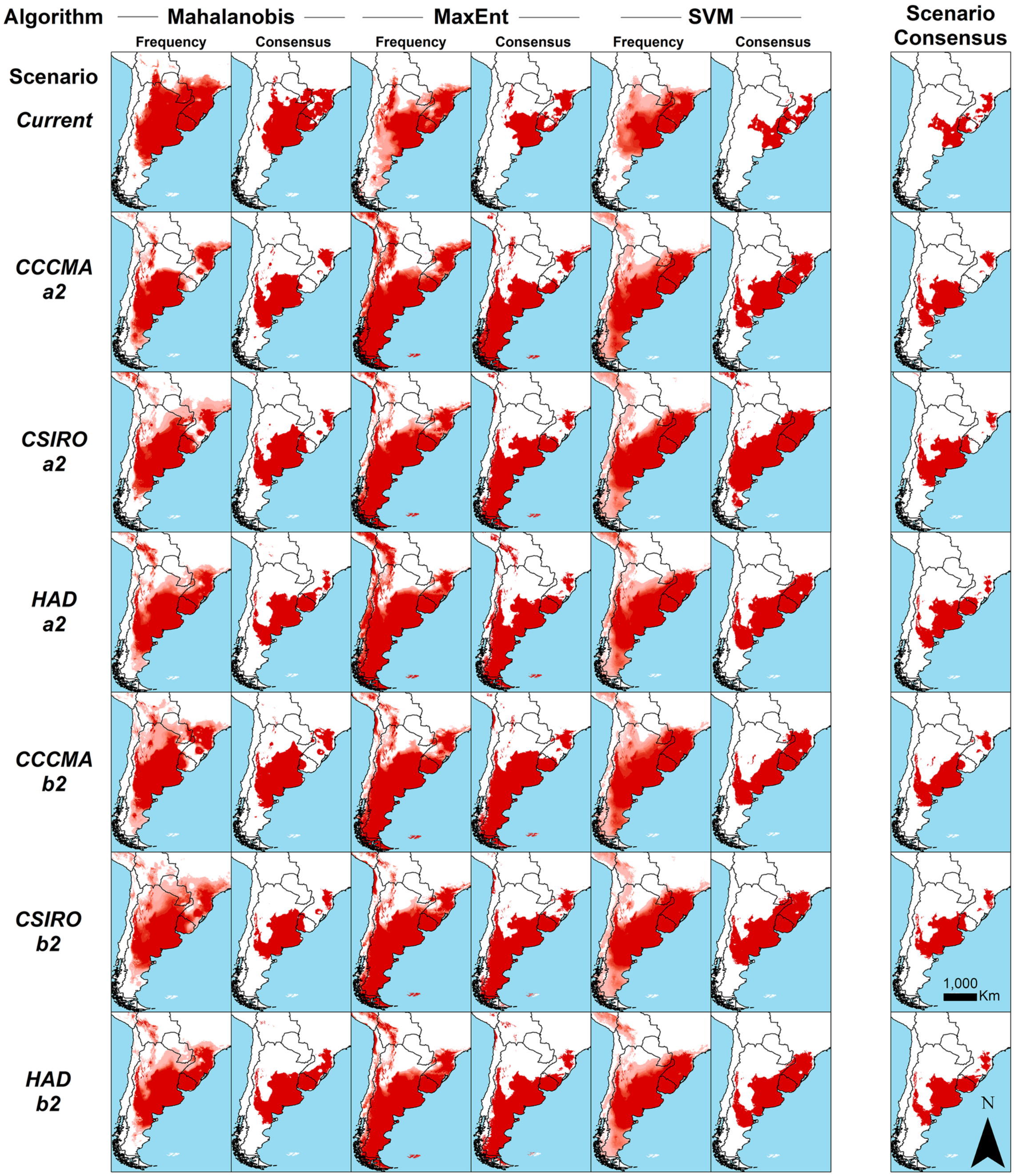

Fig. 3 *Bombus bellicosus* current and future distribution in southern South America. The figure shows three different modelling approaches based on the modelling algorithms: Mahalanobis distance, Maxent and SVM. Frequency and consensus maps are shown. Current and future scenarios were based on the 19 environmental variables from the WorldClim dataset. The future climate modelling variables were based on different Atmosphere Ocean General Circulation Models (AOGCMs) for the years 2080 (CCCMA-CGM2, CSIRO-MK2.0, and UKMO-HADCM3), considering both optimistic and pessimistic emission scenarios (B2a and A2a, respectively)

South American moths, climate change will force range shifts and reduce the conservation effectiveness of some protected areas, even leading 4 % of all analysed species to extinction (Ferro et al. 2014). The bee fauna (bumblebees included) from this region, as they are also dependent on the same environmental variables, may also show similar patterns upon future climate change scenarios.

According to our potential distribution models, the center of the original distribution of *B. bellicosus*, near Buenos Aires, Argentina (Abrahamovich et al. 2004), will be still suitable for the species in the future. Declines on bumblebee populations on the border and its persistence in areas closer to the center of their distribution was also observed in other species (Williams et al. 2007, 2009).

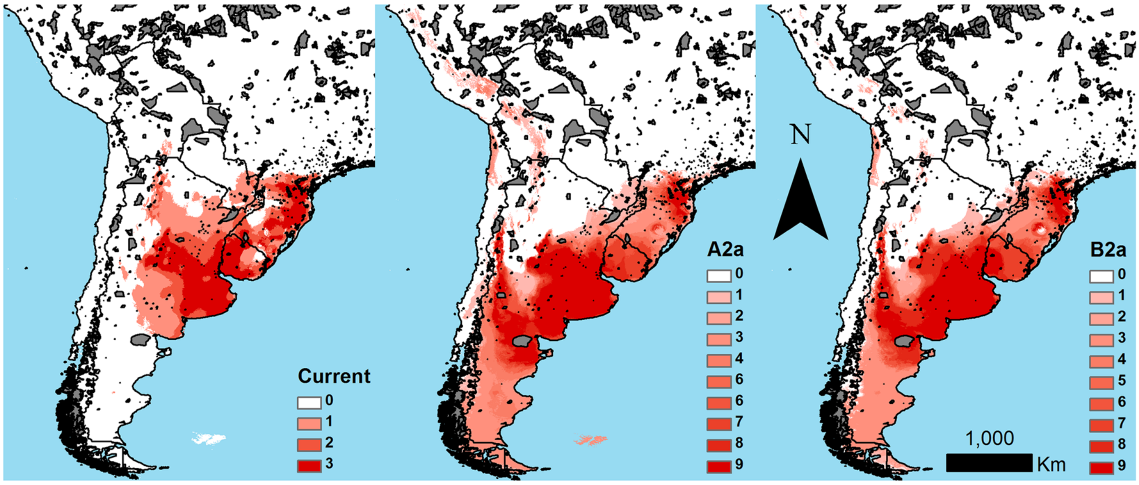

Fig. 4 *Bombus bellicosus'* current and future distributions overlapped with South American protected areas network (IUCN). The three distribution maps represents the consensual distribution all maps obtained by all three algorithms models (Mahalanobis, Maxent and SVM) in each different (Current, Pessimistic, and Optimistic) climatic scenario. The numeric scale correspond to the consensual distribution obtained by each modelling algorithm and climatic scenario. Future distributions were obtained from the mean consensus from the predicted distributions by each modelling algorithm and on the three of AOGCM for both pessimist (A2a) and optimistic (B2a) emission scenarios. Grey polygons refer to the available South American protected areas network (categories I–IV ≈ strict reserves) from the IUCN's World Database on the protected areas

Many studies show the vulnerability of species in the boundaries of their distributions, especially regarding climate change (Parmesan 2006). Climate is the main factor determining the boundaries of species distributions. It may decrease the fitness of marginal populations (Hoffmann and Blows 1994), and limit the bees' ability to adapt to potential climate change scenarios (Bridle and Vines 2007). However, some intrinsic biological traits related to *B. bellicosus* may also determine how it will behave under future climate changes.

The presence of a wax cover in nests of *B. bellicosus*, unlike other tropical and subtropical species, is a biological trait that links this species to temperate climates (Sakagami et al. 1967a; Hines et al. 2007), and allows their nests to maintain higher temperatures, especially during cold seasons. However, under future climate change scenarios and increasing environmental temperatures, this wax layer may eventually cause severe temperature increases inside nests of *B. bellicosus*. Temperature is a very important environmental characteristic for the development of all insect species (Chown and Terblanche 2006). High temperatures negatively affect the development of insect broods (Polak and Tomkins 2013). In the future, both vitality and strength of nests of *B. bellicosus* may decrease, given the expected temperature increases under future scenarios of climate change.

There is solid evidence in the literature that some invertebrate species may not cope with plant species phenological changes (Root et al. 2003; Hegland et al. 2009). Consequently, the available resources available for pollinator insect species during the most important period of their developmental stages may eventually decrease under climate warming, causing considerable problems to insect pollinators (Durant et al. 2007), especially for specialized plant-pollinators interactions (Schweiger et al. 2012). In some cases, plant species phenological advances may not cause significant problems to the insect that are dependent on them (Bartomeus et al. 2011). However, the role of plant species phenological changes on the future distribution of *B. bellicosus* may be of a smaller importance, as it is a generalist species (Arbulo et al. 2011) which visits more than 60 different plant species (Martins and Melo 2009). Consequently, eventual phenological changes of South American plant species undergoing climate change, as already reported elsewhere (Root et al. 2003; Parmesan 2006), will probably not affect the persistence of *B. bellicosus* in the considered area.

Some studies also question the association between climate change and declines in bumblebee populations (Williams and Osborne 2009) and link population declines mainly to habitat loss (Fitzpatrick et al. 2006). Other key factors, such as introduced species, pesticides and pathogens, are also claimed to have an important effect on bumblebee populations (Goulson et al. 2008). All these factors cannot be discarded in the local extinction of *B. bellicosus*, especially because intense land use and the increase of urban matrixes have been proved to influence the observed population decline for many bee species, including *B. bellicosus* in southern Brazil (Martins et al. 2013). Land use change is continuously growing in the areas occupied by *B. bellicosus* in the last four decades due to strong agricultural expansion. Such factors will continue to affect the bee fauna in the region studied unless conservation actions take place (Overbeck et al. 2007; WWF 2013). An increasing urban matrix is usually a deleterious factor for bees, although some surviving species may still persist this habitat that is inhospitable for many bee species (Winfree et al. 2007; Banaszak-Cibicka and Żmihorski 2011). Bee survival in urban environments (and other anthropogenic landscapes) depends on the availability of feeding and nesting resources within the bee's dispersal ability (Kremen et al. 2007).

Using SDMs to support decisions regarding species conservation in the future climate change scenarios is not a simple task, mainly because the resulting potential distributions (based on the current knowledge on species distribution) are impossible to be truly validated (Pearson and Dawson 2003). However, SDMs are still one of the best alternatives to discuss species conservation under future climate change (Hannah et al. 2007; Heller and Zavaleta 2009; Guisan et al. 2013). The current PA network from South America will be able to protect small disconnected portions of the distribution of *B. bellicosus* under both the current and the future climate change scenarios. Nonetheless, and given the disaggregated predicted distributions of *B. bellicosus* in southern Brazil, remnant vegetation and PAs located within this region may eventually be stepping-stones for *B. bellicosus* populations (which is fundamental in cases of climate change; Hannah et al. 2007). Stepping-stones facilitate southward dispersal, considering the future scenarios of climate change. The establishment of several new protected areas can contribute to future efforts of *B. bellicosus* conservation, although the current PA network will be able to protect some portions of the distribution of *B. bellicosus*. Protected areas on the grasslands of southern South America, which are the main habitat for *B. bellicosus*, are fundamental for the conservation of this pollinator species in particular. However, these are one of the most neglected habits in that region, often endangered by large scale livestock and crops (Overbeck et al. 2007).

The current presence of the species in a protected area does not necessarily mean it will be protected in the future, although the conservation biogeography framework considers a given species to be protected even if the smallest portion of its distribution is covered by a protected area (Rodrigues et al. 2004). The current effectiveness of a PA in protecting *B. bellicosus* (and other species as well) may vary, especially because such areas were generally created without any ecological criteria. Additionally, when we consider the future climate change scenarios, the current network of protected areas will not be enough to protect species (Hannah et al. 2007), even in an optimistic scenario. Considering this situation, future PA implementation needs to be based on ecological theories rather than only on the stakeholders' will and/or landscape scenic beauty (Hannah et al. 2007).

An additional factor which may potentially affect *B. bellicosus* and other South American bumblebees in the future is the competition for resources with *B. terrestris*, as already recently reported in Argentina (Morales et al. 2013). *B. terrestris* is a very competitive species (Goulson 2003), introduced in many regions of the world to pollinate crops, including in Chile, where it began its spread towards other South American countries, and to consequently replace both a previously introduced and a native bumblebee species (Morales et al. 2013). There is a chance that this species may continuously spread to southern and southeastern Brazil, and cause negative effects on other native bumblebees species (Saraiva et al. 2013).

In this paper we showed the potential distribution of *B. bellicosus*, under current and future scenarios of climate change, and discussed the potential influence of climate in its disappearance in some regions of Southern Brazil, where it was once the most abundant native species (40 years ago). However, the general absence of quality biological and ecological aspects of *B. bellicosus* as well as information regarding its wild populations are still major drawbacks for its efficient current and future protection. Besides its undeniable value in conservation predictions, SDMs results rarely become practical conservation decisions, mainly due to a gap in the communication between researchers (who design the models) and decision makers (Guisan et al. 2013). We hope that the results presented here may, eventually, leave the theoretical grounds and serve both conservationists and stakeholders as practical bridges towards the future protection of *B. bellicosus* in South America, especially given the potential adverse effects of climate changes for this species. Increasing the area and representativeness of protected areas, especially of the grasslands which serve as habitat for *B. bellicosus*, may have a major importance in the conservation of this and other species of Latin American pollinators in the near and potentially threatening future.

Acknowledgments ACM would like to thank all the researchers who made their Entomological Collections open-access online and provided several of the *B. bellicosus* occurrences used here. ACM would also like to thank the curators Betina Blochtein (PUC-RS) and Maria H. Galileo (Fundação Zoobotânica-RS) for allowing the exam of their collections and Rafael Kamke who personally examined *B. bellicosus* specimens in the bee collection of UFSC. We would like to thank Sara Lodi, Solana Boschilia, Victor Gonzalez, and two anonymous reviewers for critical comments on the manuscript. ACM and DPS received doctorate fellowships from CNPq—Conselho Nacional de Desenvolvimento Científico e Tecnológico (148685/2010-2 and 147204/2010-0, respectively). PDMJ and GARM have been continuously supported by grants from CNPq.

References

Abrahamovich AH, Díaz NB, Morrone JJ (2004) Distributional patterns of the Neotropical and andean species of the genus *Bombus* (*Hymenoptera: Apidae*). Acta Zool Mex 20:99–117

Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Arbulo N, Santos E, Salvarrey S, Invernizzi C (2011) Proboscis length and resource utilization in two uruguayan bumblebees: *Bombus atratus* Franklin and *Bombus bellicosus* (Hymenoptera: Apidae). Neotrop Entomol 40:72–77

Ascher JS, Pickering J (2014) Discover life bee species guide and world checklist (Hymenoptera: Apoidea: *Anthophila*). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Banaszak-Cibicka W, Żmihorski M (2011) Wild bees along an urban gradient: winners and losers. J Insect Conserv 16:331–343

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol Evol 3:327–338

Barry S, Elith J (2006) Error and uncertainty in habitat models. J Appl Ecol 43:413–423

Bartomeus I, Ascher JS, Wagner D et al (2011) Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proc Natl Acad Sci USA 108:20645–206459

Bartomeus I, Ascher JS, Gibbs J et al (2013) Historical changes in northeastern US bee pollinators related to shared ecological traits. Proc Natl Acad Sci USA 110:4656–4660

Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354

Bommarco R, Lundin O, Smith HG et al (2012) Drastic historic shifts in bumble-bee community composition in Sweden. Proc R Soc B Biol Sci 279:309–315

Bridle JR, Vines TH (2007) Limits to evolution at range margins: when and why does adaptation fail? Trends Ecol Evol 22:140–147

Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. Biol Conserv 144:2647–2655

Chapman RE, Bourke AFG (2001) The influence of sociality on the conservation biology of social insects. Ecol Lett 4:650–662

Chown SL, Terblanche JS (2006) Physiological diversity in insects: ecological and evolutionary contexts. Adv In Insect Phys 33:50–152

Colla SR, Gadallah F, Richardson L et al (2012) Assessing declines of North American bumble bees *Bombus* spp. using museum specimens. Biodivers Conserv 21:3585–3595

Colombo AF, Joly CA (2010) Brazilian Atlantic forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Braz J Biol 70:697–708

Diniz-Filho AF, Bini LM, Rangel TF et al (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32:897–906

Diniz-Filho JAF, De Marco Jr P, Hawkins BA (2010) Defying the curse of ignorance: perspectives in insect macroecology and conservation biogeography. Insect Conserv Divers 3:172–179

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

Ellis JS, Knight ME, Darvill B, Goulson D (2006) Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera: Apidae). Mol Ecol 15:4375–4386

Farber O, Kadmon R (2003) Assessment of alternative approaches for bioclimatic modelling with special emphasis on the Mahalanobis distance. Ecol Modell 160:115–130

Ferro VG, Lemes P, Melo AS, Loyola R (2014) The reduced effectiveness of protected areas under climate change threatens atlantic forest tiger moths. PLoS One 9:e107792. doi:10.1371/journal.pone.0107792

Fitzpatrick U, Murray TE, Paxton RJ, Breen J, Cotton D, Santorum V, Brown MJF (2006) Rarity and decline in bumblebees – A test of causes and correlates in the Irish fauna. Biol Conserv 136:1–10

Garratt MPD, Coston DJ, Truslove CL et al (2014) The identity of crop pollinators helps target conservation for improved ecosystem services. Biol Conserv 169:128–135

Giannini TC, Acosta AL, Garófalo CA et al (2012) Pollination services at risk: bee habitats will decrease owing to climate change in Brazil. Ecol Modell 244:127–131

Google Inc. (2013) Google Earth. version 7.0.3.8542

Goulson D (2003) Effects of introduced bees on native ecosystems. Annu Rev Ecol Evol Syst 34:1–26

Goulson D, Lye GC, Darvill B (2008) Decline and conservation of bumble bees. Annu Rev Entomol 53:191–208

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Modell 135:147–186

Guisan A, Tingley R, Baumgartner JB et al (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435

Hannah L, Midgley G, Andelman S et al (2007) Protected area needs in a changing climate. Front Ecol Environ 5:131–138

Hegland SJ, Nielsen A, Lázaro A et al (2009) How does climate warming affect plant-pollinator interactions? Ecol Lett 12:184–195

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142:14–32

Herrera JM, Ploquin EF, Rodríguez-Pérez J, Obeso JR (2014) Determining habitat suitability for bumblebees in a mountain system: a baseline approach for testing the impact of climate change on the occurrence and abundance of species. J Biogeogr 41:700–712

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hines HM, Cameron SA, Deans AR (2007) Nest architecture and foraging behavior in *Bombus pullatus* (Hymenoptera: Apidae), with comparisons to other tropical bumble bees. J Kans Entomol Soc 80:1–15

Hoffmann AA, Blows MW (1994) Species borders: ecological and evolutionary perspectives. Trends Ecol Evol 9:223–227

Jiménez-Valverde A, Peterson AT, Soberón J et al (2011) Use of niche models in invasive species risk assessments. Biol Invasion 13:2785–2797

Kamino LHY, Stehmann JR, Amaral S et al (2011) Challenges and perspectives for species distribution modelling in the neotropics. Biol Lett 8:324–326

Kearney M (2006) Habitat, environment and niche: What are we modelling? Oikos 1115:186–191

Klatt BK, Holzschuh A, Westphal C et al (2014) Bee pollination improves crop quality, shelf life and commercial value. Proc R Soc B Biol Sci 281:20132440

Klein A-M, Steffan-Dewenter I, Tscharntke T (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. Proc R Soc B Biol Sci 270:955–961

Kremen C, Williams NM, Aizen MA et al (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Lemes P, Loyola RD (2013) Accommodating species climate-forced dispersal and uncertainties in spatial conservation planning. PLoS One 8:e54323. doi:10.1371/journal.pone.0054323

Liu CR, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393

Loyola RD, Lemes P, Faleiro FV et al (2012) Severe loss of suitable climatic conditions for marsupial species in Brazil: challenges and opportunities for conservation. PLoS One 7: e46257. doi:10.1371/journal.pone.0046257

Marmion M, Parviainen M, Luoto M et al (2009) Evaluation of consensus methods in predictive species distribution modelling. Divers Distrib 15:59–69

Martins AC, Melo GAR (2009) Has the bumblebee *Bombus bellicosus* gone extinct in the northern portion of its distribution range in Brazil? J Insect Conserv 14:207–210

Martins AC, Gonçalves RB, Melo GAR (2013) Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years. Zoologia 30:157–176

MEA. (2005) Millenium Ecosystem Assessment. Ecosystems and Human well-being: Scenarios - Millenium Ecosystem Assessment—Drivers of Ecosystem Change, vol 1. Island Press, Washington, DC, pp 74–76

Michener CD (2007) The Bees of the World, 2nd ed. : p 992

Morales CL, Arbetman MP, Cameron SA, Aizen MA (2013) Rapid ecological replacement of a native bumble bee by invasive species. Front Ecol Environ 11:529–534

Moure JS, Sakagami SF (1962) As mamangabas sociais do Brasil (*Bombus*, Latreille) (Hymenoptera, Apoidea). Stud Entomol 5:65–194

Muñoz MES, De Giovanni R, de Siqueira MF et al (2011) openModeller: a generic approach to species' potential distribution modelling. Geoinformatica 15:111–135

Nóbrega CC, De Marco P Jr (2011) Unprotecting the rare species: a niche-based gap analysis for odonates in a core Cerrado area. Divers Distrib 17:491–505

Overbeck G, Muller S, Fidelis A et al (2007) Brazil's neglected biome: the South Brazilian *Campos*. Perspect Plant Ecol Evol Syst 9:101–116

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Glob Ecol Biogeogr 12:361–371

Phillips SJ, Dudik M (2008) Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259

Polak M, Tomkins JL (2013) Developmental selection against developmental instability: a direct demonstration. Biol Lett 9:20121081

Potts SG, Biesmeijer JC, Kremen C et al (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Rangel TF, Loyola RD (2012) Labeling ecological niche models. Nat Conserv 10:119–126

Rocchini D, Hortal J, Lengyel S et al (2011) Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. Prog Phys Geogr 35:211–226

Rodrigues ASL, Andelman SJ, Bakarr MI et al (2004) Effectiveness of the global protected area network in representing species diversity. Nature 428:640–643

Root TL, Price JT, Hall KR, Schneider SH (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Sakagami SF, Laroca S (1971) Relative abundance, phenology and flower visits of apid bees in eastern Paraná, Southern Brazil (*Hymenoptera*, *Apidae*). Kontyû 39:217–230

Sakagami SF, Akahira Y, Zucchi R (1967a) Nest architeture and brood development in a neotropical bumblebee, *Bombus atratus*. Insectes Soc 14:389–413

Sakagami SF, Laroca S, Moure JS (1967b) Wild bee biocenotics in São José dos Pinhais (PR), South Brazil, Preliminary Report. J Fac Sci Hokkaido Univ Ser VI, Zool 16:253–291

Saraiva AM, Acosta AL, Giannini TC et al (2013) *Bombus terrestris* na América do Sul: possíveis rotas de invasão deste polinizador exótico até o Brasil. polinizadores do bras contrib e perspect para biodiversidade, uso sustentável, conserv e serviços ambient

Schölkopf B, Platt JC, Shawe-Taylor J et al (2001) Estimating the support of a high-dimensional distribution. Neural Comput 13:1443–1471

Schweiger O, Heikkinen RK, Harpke A et al (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Glob Ecol Biogeogr 21:88–99

Serra BDV, De Marco PJ, Nóbrega CC, Campos LAO (2012) Modeling potential geographical distribution of the wild nests of *Melipona capixaba* Moure & Camargo, 1994 (Hymenoptera, Apidae): conserving isolated populations in mountain habitats. Nat Conserv 10:199–206

Silva DP, Aguiar AJC, Melo GAR et al (2013) Amazonian species within the cerrado savanna: new records and potential distribution for *Aglae caerulea* (Apidae: Euglossini). Apidologie 44:673–683

Silva DP, Gonzalez VH, Melo GAR et al (2014) Seeking the flowers for the bees: integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America. Ecol Modell 273:200–209

Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. Trends Ecol Evol 20:651–652

Stockwell DRB, Peterson AT (2002) Effects of sample size on accuracy of species distribution models. Ecol Modell 148:1–13

Tax DMJ, Duin RPW (2004) Support vector data description. Mach Learn 54:45–66

Thompson HM (2001) Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). Apidologie 32:305–321

Thomson D (2004) Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458–470

Travis JMJ (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. Proc R Soc B Biol Sci 270:467–473

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Varela G (1992a) Nota preliminar sobre la fenologia del nido de *Bombus bellicosus* Smith, 1879 (Hymenoptera, Apoidea). Bol Soc Zool Uruguay 7:53–54

Varela G (1992b) Nota preliminar sobre los componentes de un nido de *Bombus bellicosus* Smith, 1879 (Hymenoptera, Apoidea). Bol Soc Zool Uruguay 7:55–56

Walther G, Post E, Convey P et al (2002) Ecological responses to recent climatic change. Nature 416:389–395

Whitehorn PR, O'Connor S, Wackers FL, Goulson D (2012) Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science 336:351–352

Whittaker RJ, Araújo MB, Jepson P et al (2005) Conservation biogeography: assessment and prospect. Divers Distrib 11:3–23

Williams PH, Osborne JL (2009) Bumblebee vulnerability and conservation world-wide. Apidologie 40:367–387

Williams PH, Araújo MB, Rasmont P (2007) Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? Biol Conserv 138:493–505

Williams P, Colla S, Xie Z (2009) Bumblebee vulnerability: common correlates of winners and losers across three continents. Conserv Biol 23:931–940

Williams NM, Crone EE, Roulston T et al (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. Biol Conserv 143:2280–2291

Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. Conserv Biol 21:213–223

Winfree R, Aguilar R, Vásquez DP et al (2009) A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076

WWF (2013) Tropical and subtropical grasslands, savannas and shrublands: Southeastern South America: Uruguay, Brazil, and Argentina. http://worldwildlife.org/ecoregions/nt0710. Accessed 4 Feb 2013