

2 **Predicting priority areas for conservation from historical climate**
3 **modelling: stingless bees from Atlantic Forest hotspot as a case**
4 **study**

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Abstract Assuming that genetically diverse populations of bees are less likely to suffer the harmful effects of inbreeding and better able to avoid an extinction vortex related to the sex determination mechanism, the identification of putative areas in which diversity is concentrated should be focus of a discussion. Models of historical climate stability constitute an elegant manner of inferring such areas. The aim of the present study was to model the potential distribution of stingless bees in different periods of climate extremes of the Late Quaternary and the current day. A spatially-explicit model was designed to predict areas in which genetic diversity is putatively concentrated in an assemblage of nineteen species in the southern Atlantic Forest, Brazil. These climatically-stable areas (i.e., refuges) were mainly recorded in three portions of coastal forests in southeastern Brazil, regions that concentrate areas of high to extreme importance to the conservation of biological diversity. Such regions have differences regarding size and suitability scores and are distributed within the southern Atlantic Forest Central Corridor (SCC), as well as the northern (NSM) and southern *Serra do Mar* Corridor (SSM). Considering that refuges historically harbor high degrees of

genetic diversity, these three regions are indicated as those of high importance to the conservation of stingless bees in the Atlantic Forest.

Keywords Biodiversity prediction · Climate stability · Conservation biogeography · MaxEnt · Paleomodelling · Refuges

Introduction

Most of the Atlantic Forest in Brazil has been destroyed by human actions and extremely impacted regions are located within recognized zones of high levels of biological diversity and endemism (Fonseca 1985; Myers et al. 2000; Ribeiro et al. 2009; Sparovek et al. 2012). Most of these zones are concentrated in coastal forests, ranging from the state of Bahia to the southern portion of the state of Paraná, which is a region composed of different formations, such as mangroves, tropical and subtropical forests. Recent studies have indicated that coastal forests in this area have maintained populations of forest-dependent species through the climate oscillations of the Late Quaternary to the present day, demonstrating that these zones are ecological refuges for different species (e.g., Carnaval and Moritz 2008; Carnaval et al. 2009). Moreover, a variety of crops of human interest are concentrated in these regions, providing agricultural products for Brazil as well as other countries.

Species of stingless bees (*Meliponini*) have been studied in these areas using different approaches such as genetic diversity (Brito and Arias 2010; Tavares et al. 2013) and phylogeographical (Batalha-Filho et al. 2010) analyses. However, previous studies have not reported regions of climatic stability that historically concentrate the evolutionary history of stingless bees, i.e., areas within the

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62 Atlantic Forest in which these insects have maintained
 63 populations and high levels of genetic diversity irrespective
 64 of time and climate oscillations. The importance of iden-
 65 tifying such areas is based on the notion that populations in
 66 climatically stable regions are genetically more diverse
 67 than those in zones of instability (Carnaval et al. 2009) and
 68 that regions concentrating high levels of genetic diversity
 69 are more likely to be of importance to conservation
 70 (Rosauer et al. 2009). Highly heterozygous populations
 71 have a better chance of success than homozygous popula-
 72 tions due to less exposure to the harmful effects of in-
 73 breeding (Frankham et al. 2004; Templeton 2006), for
 74 example. Moreover, the production of sterile or unviable
 75 diploid males due to homozygosity at a single sex locus in
 76 haplodiploid species is considered a serious factor for ini-
 77 tiating an extinction vortex in populations of Hymenoptera
 78 impacted by habitat change (Zayed and Packer 2005). In
 79 light of the few fragments of the Atlantic Forest remaining
 80 and the well-known importance of stingless bees as polli-
 81 nators of crops (Heard 1999), the determination of areas in
 82 which the evolutionary history of such bees is concentrated
 83 should be the focus of discussion.

84 An elegant approach to predicting regions with a high
 85 concentration of diversity, especially genetic diversity, is
 86 based on the elaboration of historical climate models
 87 through ecological niche modelling (Hugall et al. 2002;
 88 Waltari et al. 2007; Carnaval et al. 2009). Such modelling
 89 allows the prediction of areas that maintained environ-
 90 mental conditions favorable for the occurrence of a target
 91 taxon irrespective of global climatic oscillations in a
 92 specific time span. Regions of stability (i.e., refuges) have
 93 demonstrated high phylogeographic predictions, as they
 94 have probably harbored a significant portion of populations
 95 and genetic diversity through the Last Inter Glacial period
 96 [120 thousand years before present (kybp)], the Last Gla-
 97 cial Maximum (21 kybp), the Mid-Holocene (6 kybp) and
 98 the present day (see Carnaval et al. 2009; Martins 2011).

99 Some studies use techniques of ecological modelling to
 100 propose priority areas for conservation basing on both
 101 current and future scenarios (Embert et al. 2011; Giannini
 102 et al. 2012, 2013; Giovannini and Seglie 2014). High
 103 richness and abundance levels of target taxa are key pre-
 104 dictors for the inference of areas to protect in these studies.
 105 We propose here an alternative method for this end by
 106 combining past and present data to infer climate stability
 107 for different species of an assemblage. This approach
 108 permits the construction of models in which both these
 109 variables (richness and abundance) as well as genetic di-
 110 versity levels are considered.

111 The principal aim of the present study was to indicate
 112 regions within the southern Atlantic Forest where the
 113 evolutionary history of stingless bees is possibly concen-
 114 trated. For such, occurrence data obtained from network

115 databases and personal surveying data were used to build
 116 stability models for nineteen species during climatic ex-
 117 tremes of the Late Quaternary. The results of all species
 118 were superimposed in a single composite model (assem-
 119 blage-scale model of climate stability), which indicates
 120 regions in which most of these taxa have putatively
 121 maintained populations irrespective of time and climatic
 122 conditions. The findings may be an important reference for
 123 future studies on population genetics, phylogeography and
 124 comparisons regarding local and regional diversity.

125 Materials and methods

126 Defining taxa and study area

127 To build a reliable model of climate stability in the Atlantic
 128 Forest, occurrence data on thirty-five species of stingless
 129 bees in the entire biome were searched using the digital
 130 platforms *speciesLink* network (www.splink.org.br) and
 131 Global Biodiversity Information Facility (GBIF, www.gbif.org)
 132 and personal data. From these data, species for which
 133 information was found encompassing a realistic panorama
 134 of the current distribution were selected. However, most of
 135 the occurrence data is concentrated in southeastern Brazil
 136 and the scarcity of data from the northern portion of the
 137 Atlantic Forest limited the analyses to the southern portion
 138 of the biome. Although these species exhibit an enormous
 139 variety of ecological and behavioral characteristics, they
 140 co-occur in the study area mostly within fragments of the
 141 Atlantic Forest. In addition, since some species also occur
 142 in other biomes (e.g., the Amazon Forest), the occurrence
 143 data were filtered and only those referring to the entire
 144 Atlantic Forest and contiguous areas were used in the
 145 analyses. This step was important to reduce the effects of
 146 niche expansion and biases resulting from background
 147 extension on the output of the model (Anderson and Raza
 148 2010). Thus, the final set of taxa in the present study was
 149 based on 493 points of occurrence for nineteen species
 150 from twelve genera of stingless bees (Table 1).

151 The following collections provided information for *spe-*
 152 *ciesLink* and GBIF regarding the points of occurrence for the
 153 nineteen species used in the present study: Coleção Ento-
 154 mológica Paulo Nogueira-Neto-IB/USP; UFES (Coleção
 155 Entomológica da Universidade Federal do Espírito Santo);
 156 Coleção DSEC Entomologia (Coleção Entomológica do
 157 Depto. de Sistemática e Ecologia/UFPB); Coleção de Hy-
 158 menoptera do INPA; Laboratório de Ecologia e Biogeografia
 159 de Insetos da Caatinga (UFCG); Coleção Camargo (RPSP);
 160 Coleção de Abelhas do Museu de Ciências e Tecnologia da
 161 PUCRS; Coleção de Entomologia do Museu de História
 162 Natural Capão da Imbuia; Coleção Entomológica Moure and
 163 Costa (EBDA); Museu de Zoologia/Universidade Estadual

Table 1 Number of occurrence points regarding distribution of the 19 stingless bees in southern Atlantic Forest

Taxa	Number of occurrence points
<i>Cephalotrigona capitata</i>	14
<i>Frieseomelitta varia</i>	8
<i>Geotrigona subterranea</i>	36
<i>Melipona bicolor</i>	28
<i>Melipona quadrifasciata anthidioides</i>	37
<i>Melipona quadrifasciata quadrifasciata</i>	11
<i>Melipona scutellaris</i>	24
<i>Nannotrigona testaceicornis</i>	21
<i>Oxytrigona tataira</i>	18
<i>Paratrigona subnuda</i>	8
<i>Partamona helleri</i>	103
<i>Partamona sooretamae</i>	7
<i>Plebeia droryana</i>	16
<i>Plebeia emerina</i>	17
<i>Scaptotrigona xanthotricha</i>	11
<i>Schwarziana quadripunctata</i>	21
<i>Trigona braueri</i>	10
<i>Trigona hyalinata</i>	10
<i>Trigona spinipes</i>	93
Total	493

164 de Campinas, ZUEC Hymenoptera; Coleção Entomológica
 165 Pe. Jesus Santiago Moure (Hymenoptera)-UFPR; Coleção
 166 Entomológica de Santa Cruz do Sul-CESC and Coleção
 167 Entomológica dos Campos Gerais do Paraná-UEPG, CECG.

168 **Ecological niche modelling (ENM)** 169 **and paleomodelling**

170 Climatic stability models were built using the maximum
 171 entropy algorithm implemented in MaxEnt (Phillips et al.
 172 2006), which is a technique that has performed as well or
 173 better than alternative methods of ecological modelling in
 174 recent comparisons (Elith et al. 2006; Hernandez et al.
 175 2006; Carnaval and Moritz 2008; Wisz et al. 2008). The
 176 approach consists of the use of occurrence data for the
 177 target species, limiting the analysis to the study area to
 178 diminish the effects of biases resulting from niche expan-
 179 sion and background extension on the output of the model
 180 (Anderson and Raza 2010), and bioclimatic variables, such
 181 as annual mean temperature and precipitation seasonality
 182 (Table S2), to build the ecological niche models. The en-
 183 vironmental descriptors employed were based on 19 bio-
 184 climatic variables (Table S2) referring to two periods of
 185 climatic extremes in the past [Last Interglacial (120 kybp)
 186 and the Last Glacial Maximum (21 kybp)] and the current

day. This information is available in the WorldClim data-
 base (www.worldclim.org). Thirty percent of the occur-
 rence data from each species were randomly chosen during
 the training of the data and used as information to test the
 models, following Rosauer et al. (2009). A combination of
 quadratic, product, threshold and hinge features was used
 to build the models, with the regularization multiplier equal
 to 1 and a maximum of 500 iterations.

We excluded variables after performing multivariate
 analyses for each species occurrence point values through
 PAST (Hammer et al. 2001). This procedure was based on
 Principal Component Analysis (PCA) and permitted the
 identification of closely related bioclimatic variables that
 potentially cause over-predictions on the model outputs.
 We extracted values of occurrence points referent to each
 19 bioclimatic variables using ArcMap 10.1. Then, we built
 a correlation matrix to access the scatter PCA diagram and
 the superimposed variables were checked as their per-
 centage contribution in the output model generated by
 MaxEnt. We excluded those variables with lower contri-
 butions and built the final model. The parameters used to
 build the final model for the current day were used during
 the projections into past conditions (i.e., 120 and 21 kybp).

After modelling the potential distribution of each spe-
 cies in the three periods, suitable areas with favorable en-
 vironmental conditions referring to each species were
 superimposed. This permitted the determination of areas in
 which each species probably found favorable environ-
 mental conditions for its occurrence irrespective of global-
 scale climate oscillations (Hugall et al. 2002). Finally, all
 the stability models referring to the nineteen species of
 stingless bees were overlaid in a single map to show pre-
 dictable areas of high importance to the conservation of the
 assemblage studied. This step differs from previous studies
 by combining climate stability paleomodels of different
 species in a single composite model.

It is worth stressing that as the value of Area Under the
 Curve (AUC) increases the performance of a given model
 is enhanced. Thus, models with an AUC higher than 0.9
 can be considered reliable predictors of favorable condi-
 tions for the occurrence of a species (Giannini et al. 2012,
 2013). However, other approaches are also described for
 this purpose, such as the comparison of the AUC and the
 10th percentile thresholding rule (=10 percentile training
 omission of MaxEnt), which denotes suitability by using
 the lowest value assigned to any of the 90 % of the records
 with the highest scores using different regularization mul-
 tiplier combinations (Pearson et al. 2007; Soley-Guardia
 et al. 2014). However, such comparisons might be very
 time consuming in large datasets and analyses of assem-
 blages. Moreover, a model using only AUC values as
 support is considered reliable. Important studies on bees
 have made use of only this estimate to validate ecological

240 niche models in recent analyses (e.g., Giannini et al. 2012,
241 2013). Thus, the decision made was only to use AUC
242 values in the present study. For a more complete expla-
243 nation regarding the importance of AUC in ecological
244 niche modelling, see Giannini et al. (2012).

245 Results

246 The potential distribution modelling of the nineteen species
247 of stingless bees showed that all the AUC training values
248 were higher than 0.907 (Table S3). Stability zones were
249 found in the southern Atlantic Forest for eighteen of the
250 nineteen species (Fig. 1). There was no evidence of puta-
251 tive refuges only for *Melipona scutellaris* in the study area.
252 This species is native from northeastern Brazil (Camargo
253 and Pedro 2007) and is not likely to occur in this region due
254 to the low degree of suitable environmental conditions,
255 despite its occurrence in areas in which it has been intro-
256 duced in the state São Paulo (southeastern Brazil) in the
257 last fifteen years (Alves et al. 2011). Small refuges were
258 shown for *Scaptotrigona xanthotricha*, but ample and
259 noteworthy areas of stability were found for the other
260 seventeen species in the three periods studied (hot colors
261 on the maps in Fig. 1).

262 Interestingly, areas of high environmental suitability at
263 the present time for some species (e.g., *Frieseomelitta*
264 *varia*, *Oxytrigona tataira* and *Paratrigona subnuda*) did
265 not figure as refuges; a result of dramatic alterations in the
266 distribution that the environments occupied by these bees
267 apparently have passed during climatic oscillations, espe-
268 cially in the Last Glacial Maximum (21 kybp). Also, spe-
269 cies for which suitable areas for occurrence in the Brazilian
270 savannah were presented mostly have refuges in the At-
271 lantic Forest, as represented in the maps of the species
272 *Cephalotrigona capitata*, *Geotrigona subterranea*, *Meli-*
273 *pona quadrifasciata anthidioides* and *Trigona spinipes*.

274 It is remarkable that the refuges were mostly recorded in
275 the coastal portions of the study area. When the nineteen
276 species stability models were superimposed on a single
277 map, stability zones were found in these regions (Fig. 2,
278 Movie S1). The same result is seen for the composite
279 model built without the exclusion of redundant variables
280 for each species model (data not shown). Three regions
281 have putatively concentrated favorable environmental
282 conditions for most species, the smallest occurring in the
283 southern Central Corridor (SCC) of the Atlantic Forest and
284 the other two distributed throughout the *Serra do Mar*
285 Ecological Corridor. These climatically-stable zones have
286 differences in size and suitability. The northern *Serra do*
287 *Mar* (NSM) is the more suitable, medium-sized refuge and
288 the SCC is a less suitable, smaller refuge. The refuge in the

southern *Serra do Mar* (SSM) is the widest of the three and
289 also has a considerable number of suitable areas (Fig. 2a).
290

291 Many suitable areas predicted in the model are found
292 within conservation units, especially in the SSM (Fig. 2b).
293 However, the opposite is seen in the SCC, where only one
294 national park (i.e., *Parque Nacional do Caparaó*) is found
295 within an area of high to extreme biological importance. In
296 contrast, seven conservation units are found in the NSM,
297 which is a region mostly embedded in the *Serra dos*
298 *Órgãos* hills: *Parque Estadual do Desengano*, an eco-
299 logical station (*ESEC do Paraíso*), three environmental
300 protection areas (*Região Serrana de Petrópolis*, *Floresta*
301 *do Jacarandá* and *Frades*) and two biological reserves
302 (*Poço das Antas* and *Tinguá*). The NSM stability zone in
303 the state of Minas Gerais (MG) in the easternmost portions
304 of the *Serra da Mantiqueira* Hill and the Ibitipoca region,
305 on the other hand, has no conservation units.

306 Discussion

307 Comparing the map of observed diversity in Fig. 1 to the
308 assemblage-scale stability map in Fig. 2a, the use of eco-
309 logical niche modelling is an efficient predictor of diversity
310 in areas with fewer sampling efforts. Note, for example,
311 that regions in the states of Rio de Janeiro (RJ) and Espírito
312 Santo (ES) are less diverse in terms of observed species
313 richness than those in the state of São Paulo (SP) (observed
314 diversity map in Fig. 1), but stability is seen in these two
315 regions as well (Fig. 2a). Since environmental conditions
316 in areas of little sampling are inputted in the analyses, the
317 suitability scores in these areas can be explored in the
318 models. This considerably diminishes possible biases
319 generated from differently sampled regions on the output
320 of each species. Moreover, the high AUC scores reflect the
321 accuracy of the models as predictors of environmental
322 conditions for each taxon to occur. In fact, MaxEnt pro-
323 vides outputs on the distribution of environmental condi-
324 tions in which each species could occur, not the actual
325 occurrence of the species—unless dispersal events and
326 biotic interactions were not factors constraining distribu-
327 tion (Anderson and Raza 2010). By superimposing the
328 stability maps of each species, therefore, a reliable model
329 was obtained to predict the environmental conditions
330 suitable for the occurrence of most stingless bees during
331 climatic extremes of the Late Quaternary and the present
332 day.

333 Considering the hypothesis that these areas of stability
334 have harbored populations with high levels of genetic di-
335 versity during periods of striking climatic alterations, the
336 evolutionary history of stingless bees in the southern At-
337 lantic Forest could be mainly concentrated in these three

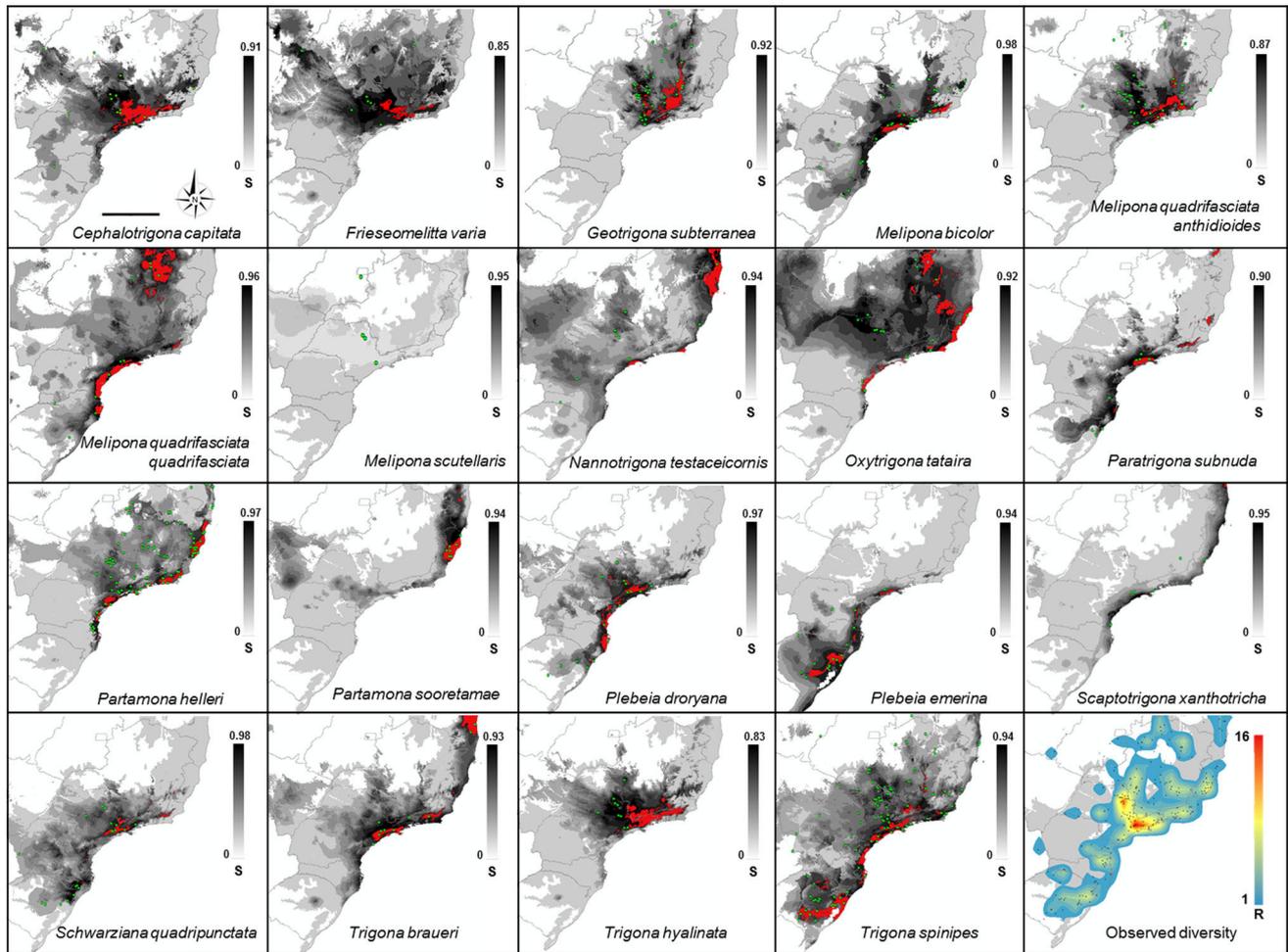


Fig. 1 Ecological niche models (gray to black) and climatically stable areas (orange to red) referring to nineteen species of stingless bees in the southern Atlantic Forest. Aiming to show only highly-suitable areas of stability, only suitability levels higher than 85 % are

provided in the maps. Observed diversity in the last square refers to richness (R) of all the nineteen species obtained in the *speciesLink* network database. Scale bar = 500 km; S = environmental suitability. Colours refer to online version only

338 montane areas (SCC, NSM and SSM). Moreover, the high
 339 levels of genetic diversity predicted by such results are an
 340 indication that the conservation of these areas should be a
 341 priority for the maintenance of heterozygous populations of
 342 stingless bees in the biome. Unfortunately, there are no
 343 robust data on the population genetics of stingless bees to
 344 test these predictions through genetic approaches. Comparing
 345 populations from climatically stable regions to those
 346 from outside refuges, one would naturally expect popula-
 347 tions from former regions to concentrate higher levels of
 348 both genetic diversity and endemism for evolutionary his-
 349 tory. However, such tests should be carried out indepen-
 350 dently. That is, spatially explicit hypotheses on taxon
 351 stability should be tested through genetic diversity and
 352 demographic tests for this taxon (Hugall et al. 2002; Car-
 353 naval et al. 2009). On the other hand, predictions regard-
 354 ing the concentration of evolutionary history, as made explicit
 355 in Fig. 2a, constitute an elegant hypothesis to be tested

through phylogenetic endemism analyses (Rosauer et al. 2009).

The conservation of areas where the three stability zones are embedded is recurrently indicated in studies using amphibians (Carnaval et al. 2009), bryophytes (Silva et al. 2014), and stingless bees (Batalha-Filho et al. 2010), among others. Given that southeastern Brazil is a highly impacted zone, a region with the highest human concentration in the country (Ervatti et al. 2015), and that montane forests probably harbor forest-dwelling species during glacial and non-glacial periods, the conservation of these areas is critical not only for stingless bees. It is clearly important to establish if these stability areas correspond with the distribution of other taxa; if this is so, these bees may act as an umbrella group for other organisms.

The present study is an investigation that innovates by pinpointing zones in which the evolutionary history of stingless bees is putatively concentrated and explores

Author Proof

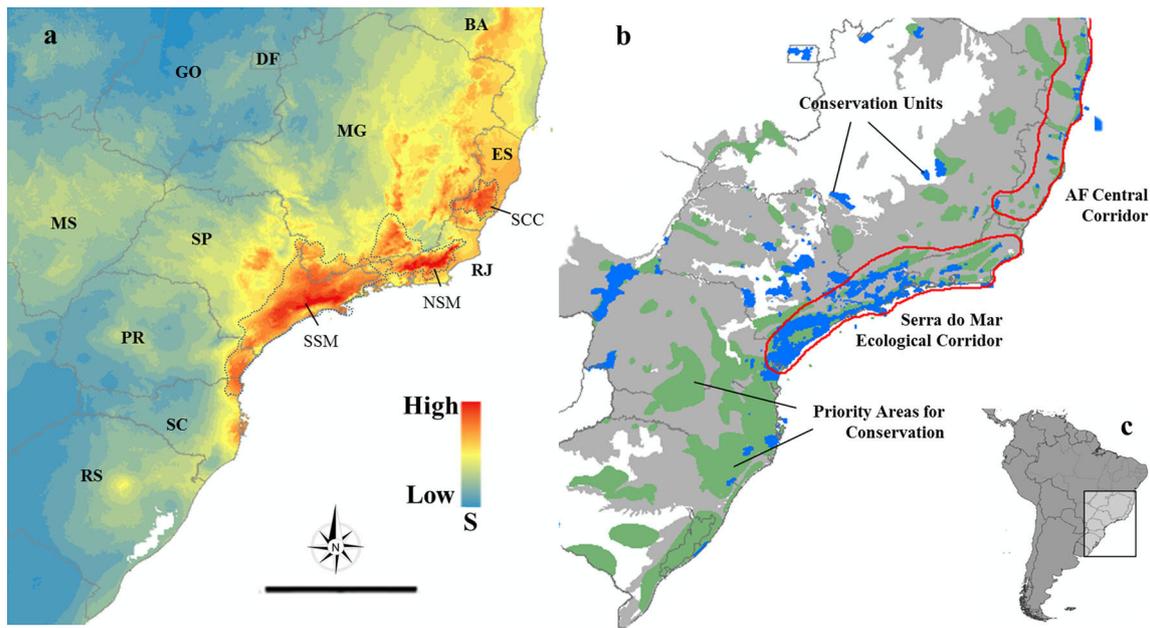


Fig. 2 Assemblage-scale model of climate stability for the nineteen stingless bee species (*a*), location of conservation units (*blue regions* in *b*) and regions of high to extreme importance to the conservation of biological diversity (*green regions* in *b*) in the southern Atlantic Forest. Stability zones in the southern Central Corridor (SCC), northern *Serra do Mar* (NSM) and southern *Serra do Mar* (SSM)

(*encircled zones with dotted line* in *a*) are predicted as those in which evolutionary history is putatively concentrated. These areas should be of considerable importance to the conservation of genetically diverse populations of stingless bees in the Atlantic Forest. The study area is shown in *c*. Scale bar for *a* and *b* = 500 km; S = environmental suitability. Colours refer to online version only

374 paleoclimatic models on the potential distribution of these
375 insects to indicate priority locations for conservation.
376 Considering the high dependency that humans have on
377 crops that stingless bees commonly visit and pollinate
378 (Heard 1999) and the high extinction rate predicted for
379 haplodiploid organisms due the production of sterile
380 diploid males caused by habitat loss, forest fragmentation,
381 the use of pesticides and climate change (Zayed and Packer
382 2005), the formulation of conservation strategies for the
383 protection of these bees should be the focus of serious
384 discussion.

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