



Assessing the landscape functional connectivity using movement maps: a case study with endemic Azorean insects

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Abstract

There is a vast body of literature aiming to predict, for a large number of taxa, the spatial distribution of suitable areas given the expected future changes of climatic conditions. However, such studies often overlook the role of landscape functional connectivity. This is particularly relevant for species with low vagility, as ground-dwelling insects, inhabiting areas with high human pressure due to habitat destruction and fragmentation, namely in the islands. In this study, we developed an individual-based model (IBM) that simulates individual movement according to landscape resistance and mortality probability, in order to derive the landscape movement map, and applied it to five endemic ground-dwelling insects of Terceira Island (Azores). We then confronted the movement maps of each species against the species distribution models previously developed for both current and future climatic conditions, quantifying the amount of important movement areas that are enclosed by the distribution polygons. We further sought to identify where habitat restoration would increase the overall connectivity among large habitat patches. Our results showed that, for both timeframes, the distribution models enclosed small amounts of areas predicted to be important for animal movement. Additionally, we predicted strong reductions (up to 94%) of these important areas for functional connectivity. We also identified areas in-between native forest of primary importance for restoration that may significantly increase the probability of persistence of our model species. We anticipate that this study will be useful to both conservation planners and ecologists seeking to understand species movement and dispersal both in islands and elsewhere.

Keywords Climate change adaptation · Landscape management · Individual-based model · Island ecology · Azores

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Introduction

Climate change effects together with habitat destruction and fragmentation are main stressors for biodiversity (Sala et al. 2000; Gitay et al. 2002; Travis 2003; Parmesan 2006; Rosenzweig et al. 2007), and their impacts are expected to increase significantly in the near future (Maxwell et al. 2016). While the intensification of human related activities, e.g. through agricultural intensification, is diminishing the available habitat for many species (Fischer and Lindenmayer 2007), the effects of climate change are expected to alter the current ecological conditions, which may severely affect the spatial distribution of habitat for numerous species (Mawdsley et al. 2009; Bellard et al. 2014). Overall, the quality and availability of habitat is decreasing while the climatic optimum is shifting (Garcia et al. 2014), forcing wildlife to track best environmental conditions through landscapes with fewer and more isolated habitat patches (Chen et al. 2011; McGuire et al. 2016). Hence, maintaining or improving the functional connectivity—the degree to which the landscape facilitates or impedes the animal movement (Taylor et al. 1993)—between habitat areas is critical to allow species to track rapidly changing landscapes (McGuire et al. 2016), therefore reducing their probability of extinction (Krosby et al. 2010).

On Islands, those global change effects are expected to pose a more extreme pressure (Bellard et al. 2014; Harter et al. 2015). In general, islands have their original native habitats significantly reduced due to human activities, often comprised by small and distanced patches (Borges et al. 2005; Triantis et al. 2010) that may be unreachable for species with low dispersal ability (Kier et al. 2009). For example, it is estimated that ca. 50% of ground dwelling arthropod species and subspecies inhabiting Azorean native vegetation (ca. 270 taxa), most of which endemic from Azores, might be driven to extinction mainly due to habitat destruction and climate change effects (Borges and Vieira 2010; Triantis et al. 2010). In fact, previous research on climatic-based species distribution in Azores suggested an overall high reduction and high range shift of species distributions in near future (Patiño et al. 2016; Ferreira et al. 2016). Furthermore, due to area limitation constrains, the conflicts between human activities and habitat conservation in islands may compromise conservation initiatives (Lambin et al. 2001; Jenkins et al. 2015). Therefore, it is crucial to access the landscape functional connectivity between habitat areas for multiple species and different timeframes, to identify key areas for animal movement, and thus ensuring the population persistence along time.

Landscape connectivity is usually measured recurring to computational algorithms, e.g. electric theory (McRae

et al. 2008) or least cost path approaches (e.g. Adriaensen et al. 2003). However, the majority of such algorithms rely on a simplistic premise that, in the absence of complete barriers, habitat patches are always reachable independently of the in-between land cover resistance for animal movement or the mortality risk. Moreover, they lack behaviorally movement rules, as ‘individuals’ have full knowledge of the landscape they are in (Coulon et al. 2015). Such limitations can be overcome within the individual-based models (IBM) framework, as it allows to simulate individuals in a given landscape where individual variability and local interactions are considered (McLane et al. 2011). By relying on such bottom-up approach that explicitly contemplates the components of a system (i.e. individuals as agents and landscape units as cells), one can obtain a movement probability map that emerges as the result of multiple individuals’ choices (Allen et al. 2016; Kleinmann and Wang 2017), rather than a simple flow of current (Railsback and Grimm 2011; Coulon et al. 2015). We may then consider that the movement map reflects the landscape functional connectivity, as it expresses the likelihood of each landscape unit being used or not by individuals while moving through the landscape.

IBMs have been used in a wide range of contexts in ecology and are recognized as a valuable tool in connectivity research (see Barton et al. 2009). Yet, this modeling method has only recently started to be applied for such purpose (e.g. Allen et al. 2016). Here, we developed an IBM that simulates animal movement conditioned by land cover resistance, slope and mortality; and applied it to five ground-dwelling endemic insect species inhabiting the Azorean archipelago. The main goal of this study was to assess the functional connectivity and highlight key areas for animal movement, under current and future climatic scenarios. The model is spatially explicit, adjustable and parameterized, so that different landscapes and species attributes can be displayed and studied. We therefore anticipate that this study will be useful to both conservation planners and ecologists and conservation researchers, who seek to understand species movement and dispersal both in islands and elsewhere.

Materials and methods

Study area and model species

The Azorean archipelago is located in the North Atlantic and is composed by nine islands with a total area of 225,000 hectares. The present study was focused on Terceira Island, the third biggest island of the archipelago, with approximately 40,200 hectares (Fig. 1). Native vegetation covers 14% of the island (Fig. 1) and is dominated by “*Juniperus-Ilex* Montane Forests” and “*Juniperus* Montane Woodlands” (Elias et al.

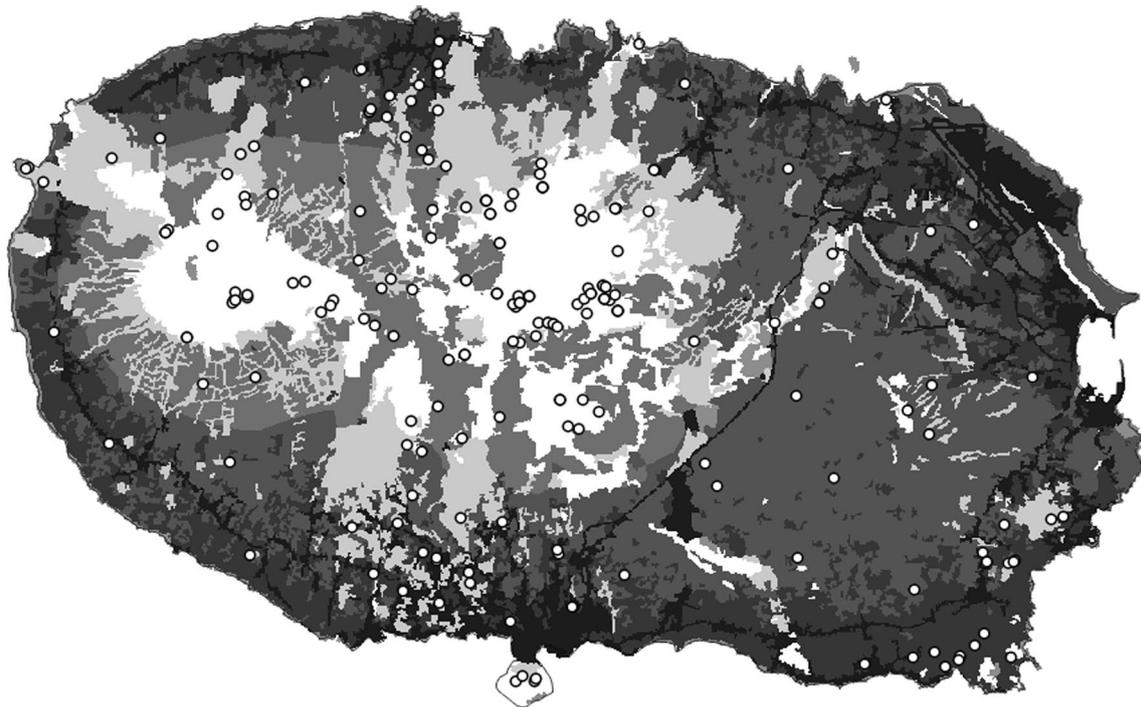


Fig. 1 Land cover of Terceira Island. Urban sites and agriculture occupy the periphery of the Island, while intensive grasslands, exotic forest, semi-natural grasslands and native vegetation are mainly located in the interior of the Island. The remaining land covers (i.e.

lagoons and open areas) occupy small areas and are not visible in the figure. White dots represent the sampling sites of pitfalls used for model validation ($n = 182$). See text for further details

2016). These native forests are luxuriant and include bryophyte communities and several species of sclerophyllous, and microphyllous trees and shrubs (Gabriel and Bates 2005; Elias et al. 2016). Such areas are known to harbor most of the native and endemic arthropod species from Azores (Cardoso et al. 2009, 2013; Florencio et al. 2016). The island has two mountains, Serra de St. Bárbara (west side) and Biscoito da Ferraria (center-east side), where the highest points are located (1020 and 830 m above sea level, respectively). Such high altitudes associated with the relatively small area imply steep slopes in some regions of the island.

The climate in the island is ‘oceanic’, with more intense characteristics from east–west and with altitude (Azevedo 2014). At sea level, the annual average air temperature is around 17.0 °C, the relative air humidity is ca. 80%, and the average annual precipitation is ca. 1000 mm. There is strong evidence that climate conditions are changing: the maximum and minimum temperatures have been rising at a rate of 0.05 and 0.36 °C per decade, respectively, from 1975 to 2002 (Miranda et al. 2006). In fact, it is expected that under the Representative Concentration Pathways 8.5 (RCP8.5) scenario, the most severe but yet realistic scenario of climate change (van Vuuren et al. 2011), in 2100 the temperature will be 2.7 °C higher and the precipitation lower by 35 mm (Azevedo and Reis 2016).

Five ground-dwelling insect species, endemic of Terceira, were selected for modeling procedures, covering a gradient of dependence of the native vegetation. Furthermore, the last four were recently assessed by IUCN as threatened (see for details <http://www.maiisg.com> and Borges et al. 2017). We summarized in the Table 1 the information for each focal species.

Individual-based model

The IBM presented here was developed in NetLogo (Wilensky 1999) and the terminology used is in accordance to the software language (e.g. agents are individuals, patches are cells). The model simulates the movement of individuals based on random walk conditional on probabilities of movement and mortality. It requires one or more layers of probabilities of movement, for example based on the resistances of land cover classes or orography. For each landscape cell, the overall probability of use (P) is the product of the different probabilities:

$$P = \prod_{i=1}^N p_i$$

where $i = 1 \dots N$ represents the different environmental factor considered. The probability of mortality for each cell (M)

Table 1 Summary of the five ground-dwelling insect species used in the present study

Species	Ecology
<i>Alestrus dolosus</i> (Crotch, 1867)	Saproxyllic click-beetle. Associated with the bark of <i>Juniperus brevifolia</i> . Occurs also in open areas of semi-natural grassland (Nardi and Mico, 2010)
<i>Aphrodes hamiltoni</i> (Quartau & Borges, 2003)	Leafhopper. Phytophagous species that inhabits the soil litter (Quartau and Borges, 2003)
<i>Drouetius borgesii borgesii</i> (Machado, 2009)	Weevil. Feeds on the leaves of several endemic trees (e.g. <i>Laurus azorica</i>) (Machado, 2009)
<i>Cedrorum azoricus azoricus</i> (Borges & Serrano, 1993)	Predatory. Restricted to <i>Juniperus-Ilex</i> Montane Forests in ravines (Borges et al., 2006)
<i>Trechus terrabravensis</i> (Borges, Serrano & Amorim, 2004)	Predatory. Restricted to <i>Juniperus-Ilex</i> Montane Forests in ravines (Borges et al., 2006)

All species belong to order Coleoptera except *A. hamiltoni* (Hemiptera). Species are sorted according to an endemic habitat dependence gradient, with more generalist species in top and specialists in bottom rows. Nothing is known about dispersal ability of studied species

is set as $1 - P$. Hence, individuals stepping into less suited patches have higher chances of being killed. In each simulation step, individuals move to one of the eight neighbors (the surrounding patches) according to P , using a roulette wheel selection (weighted probability). Yet, to avoid loop movements, the probability of reusing a used patch is diminished by setting the weight associated to that patch to zero. The model can be fed with other layers of environmental importance, for example regions with suitable climatic conditions; and can identify clusters of highest suitable habitat.

The model allows performing two types of simulations. In the first type (Sim1), agents are spread randomly throughout the landscape and they move until their death. Each patch registers the agent identity ID that stepped into it, and after a sufficient number of agents being launched, the output is a landscape movement map indicating where the movement is more likely to occur. In the second simulation type (Sim2), the model loads one single agent in every patch located in the edge of the clusters of highest suitable habitat, which we set to be areas of native vegetation. We further restricted the agents to be loaded only inside areas of climatic suitability, according to work of Ferreira et al. (2016). Again, when agents are moving, each patch registers the identities of agents that stepped into it, but this information is retained only for those agents that successfully reach a different cluster. Hence, this second simulation type allows the detection of important corridor areas for maintaining or improving the functional connectivity between clusters of native vegetation areas. See the overview, design concepts, and details protocol (ODD) (Grimm et al. 2006, 2010) protocol for a full description of the model and simulation types in the Supplementary Material S2.

Environmental information

We derived the probability of movement P based on the resistance of land cover and terrain slope. We used the most

recent land cover information available (DROTRH 2008). The layer was further corrected from field work observations to include information regarding the localization of semi-natural and intensive grassland (Cardoso et al. 2013). The terrain slope was obtained from the digital elevation model (USGS 2015) using the QGIS Slope tool (QGIS Development team 2016). We aggregated both layers to 100 m resolution due to computational limitations. In order to derive the probabilities of movement, we inquired all three researchers working with these species about the most likely value of resistance. Each expert assigned species-specific values for both layers based on their experience and knowledge from field work. These values were then combined into a single value by median (see below and Supplementary Material S1).

We also used the layers of climatic suitable areas for the focal species for current and future conditions as data for the potential distribution (Ferreira et al. 2016). In that study, the authors used the scenario RCP8.5 to derive the climatic suitability for both current (1961–1999) and future conditions (2080–99). We used these suitability models to delimit the area of connectivity analysis and to obtain the most probable movement area of each focal species, for both current and future climate conditions.

Output data treatment

Regarding the first set of simulations (Sim1), the movement suitability maps were classified into three classes according to the proportion of agents that used them: ‘medium’, ‘high’ and ‘top’, respectively for those cells with proportion of use within the percentiles [75–85], [85–95], and [95–100]. The use of such classification, although somehow subjective, was meant to easily identify the most important areas for movement. We then overlapped the movement maps with the climatic suitability areas to assess the quality of the functional

connectivity inside the expected areas of distribution (current and future timeframes).

For the second set of simulations (Sim2), we identified the most important sites to restore, i.e. key corridor or stepping-stone cells, by calculating the patch importance of matrix cells (I) as follows:

$$I = \log(u + 1) \times d^2$$

where u is the use of the matrix cell (the number of different agents that used a specific cell and reached a different cluster from which they were created), and d represents the distance of the cell to the nearest cluster. We further considered only those cells with I higher than percentile 95 of all I 's for each species. We finally derived the multi-specific priority stepping-stones by overlaying the resultant maps across species.

Model validation

An important step when using the IBM approach is the validation. Ideally, we would have parameterized the probability of movement using empirical data, namely tracking information (e.g. Youngquist and Boone 2014). However, such data is inexistent for our study area, and the information available for our study species is scarce. Hence, in order to provide an assessment of the robustness of our approach, we compared the movement maps from the first set of simulations (Sim1) with empirical data of species occurrence. This dataset consists of pitfall data from 182 sites spread throughout the island (Fig. 1), and surveyed for over 10 years (Borges et al. 2005; Cardoso et al. 2009). The data was reclassified to presence-absence data given the low number of pitfalls with occurrences of our focal species (*Alestrus dolosus*, $n = 13$; *Aphrodes hamiltoni*, $n = 53$; *Cedrorum azoricus azoricus*, $n = 10$; *Drouetius borgesii borgesii*, $n = 17$; *Trechus terrabravensis*, $n = 9$). We assumed that a higher probability of occurrence in a given site was related to a higher likelihood of that site being used for movement.

The comparison of occurrence patterns with the movement maps was performed using two different procedures. In the first, we randomized the resistance values of the land

cover classes and slope, therefore generating landscapes ($n = 1000$) with random probability of use (P) and mortality (M), and replicated the procedure used for the first set of simulations (Sim1). We expected that the simulations fed with resistance values derived from expert knowledge would outperform the random combinations when faced against empirical occupancy patterns. Binomial generalized linear models (GLM) were used to relate the presence/absence empirical data with the movement maps (expert-based and with random combinations). We expected that the GLM using the expert-based map would provide higher goodness-of-fit, here measured using the McFadden's pseudo R^2 , for more than 95% of simulations using random combinations. For the second procedure, we compared the movement maps with those produced by two commonly used algorithms for studying functional connectivity, namely CIRCUITSCAPE (McRae et al. 2008) and least-cost path (LCP, Adriaenssen et al. 2003). Likewise, we expected that the GLM using the expert-based map would provide higher goodness-of-fit relatively to those when using those two alternative algorithms.

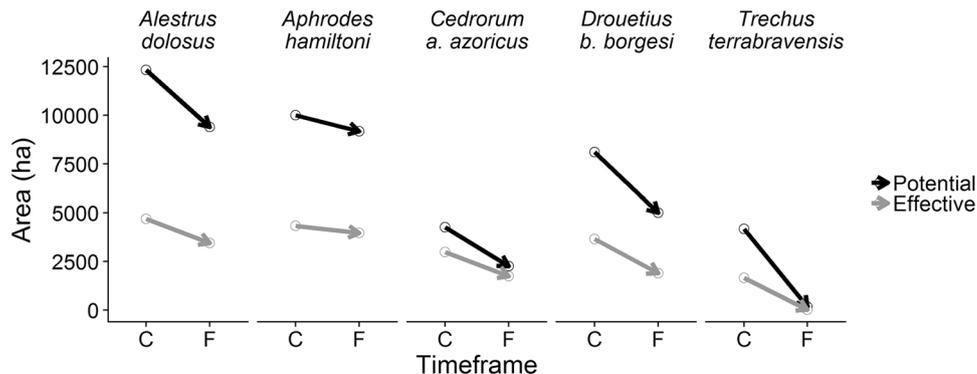
All analyses and plots were made in R environment (R Core Team 2015) and in ArcGIS (version 10.5.1). LCP was calculated using the R package 'gDistance' (van Etten 2017).

Results

The movement maps based on expert knowledge outperformed those using randomly assigned resistances for all species (Table S3.1). This result supported the use of resistances based on expert knowledge. Also, given the purpose of generating a movement map, the IBM outperformed the other algorithms for all the studied species (Table S3.2).

Areas with higher movement quality covered a small proportion of the potential area of distribution, with exception for *C. a. azoricus*. This species, for being climatically restricted to the areas with native vegetation (hence having the lowest amount of potential area of distribution), the proportion of higher movement quality was found to be the highest (Fig. 2, Figs. S4.1, S4.2). Excluding *C. a. azoricus*,

Fig. 2 Amount of potential and effective areas for animal movement for current (C) and future (F) climatic conditions, per species. 'Potential' areas refer to the most probable area of distribution previously modeled, based only on climatic conditions (Ferreira et al. 2016). 'Effective' areas are the amount of higher quality connectivity areas ('high' and 'top'; see text for details) within the most probable area of distribution



for current climatic conditions, the high and top quality areas represented around 40% of the most probable area of distribution. By the end of the century, these areas are expected to suffer a significant reduction, particularly in *T. terrabravensis*, for which <6% of the projected climatic suitable area will remain of higher quality (Fig. 2). Moreover, in absolute terms, *A. dolosus* and *A. hamiltoni* showed higher areas of movement quality inside potential areas of distribution, for both considered periods.

We detected key areas that may increase the movement between most suitable habitat areas (Sim2) (Supplementary Material S4). Under the current climatic conditions, all species but *C. a. azoricus* showed a relatively high capacity to exchange individuals among native sites, being *A. dolosus* the species with the highest dispersal capacity (Table 2). Under the future climate scenario considered, *A. dolosus*, *A. hamiltoni* and *D. b. borgesii* were found to maintain their ability to disperse to other native sites. On the other hand, *C. a. azoricus* and *T. terrabravensis* presented high reductions in the total number of individuals that disperse to another native site (Table 2). Such results are also in accordance with the spatial location of the corridors between timeframes, where more changes can be observed for *C. a. azoricus* and *T. terrabravensis*. Overall, the location of priority sites for improving the functional connectivity remained essentially the same between present and future climatic conditions (identified as A and B in Fig. S4.8) and can therefore play an important role connecting Biscoito da Ferraria and Serra de St. Bárbara (see Fig. S4.8).

Discussion

We assessed the functional connectivity of Terceira Island by deriving the movement probability based land cover and slope resistances. According to our results, the area with higher likelihood of being used for animal movement currently occupies a small proportion of the species distribution. Yet, we estimated that this proportion will further decrease according to the projected distribution areas.

Table 2 Total number of individuals per species and timeframe that successfully migrate between native vegetation areas (with percentage of successful migrations between parentheses)

Species	Current	Future
<i>Alestrus dolosus</i>	36,689 (0.29)	38,102 (0.35)
<i>Aphrodes hamiltoni</i>	38,645 (0.35)	39,951 (0.39)
<i>Cedrorum azoricus azoricus</i>	2982 (0.078)	421 (0.021)
<i>Drouetius borgesii borgesii</i>	34,685 (0.39)	23,078 (0.38)
<i>Trechus terrabravensis</i>	35,823 (0.87)	556 (1.39)

Note that the total number of individuals generated varied between species and timelines

This suggests that the functional connectivity can be seriously compromised due to climate change effects. Previous research predicted an overall loss of suitable areas in order of 90–100% for a large number of Azorean arthropods (Ferreira et al. 2016). Here, we show that functional connectivity will likewise suffer significant reductions, particularly for species like *T. terrabravensis*. Moreover, assuming that other small sized species in Azores face similar threats (Triantis et al. 2010; Cardoso et al. 2013), our results suggest that many species will lose a great proportion of high quality areas for movement. On the other hand, the sea level rise is expected reduce the available land area to be shared by all species and individuals (Mawdsley et al. 2009; Wetzel et al. 2013; Courchamp et al. 2014; Harter et al. 2015). Therefore, species range shift, as a response for climate change effects, can be seriously compromised in this island.

According to our simulations, ensuring the functional connectivity between native vegetation areas should be a priority as an adaptation response to climate change effects (Gaspar et al. 2011; McGuire et al. 2016). Given the conflicts between human activities and conservation (see e.g. Lambin et al. 2001; Jenkins et al. 2015), which are more prone to occur in small areas (such as small islands), our study provides important information on where to implement management actions to restore or improve the landscape functional connectivity. These sites should be considered for restoration, as they are likely to facilitate the dispersion for the majority of ground-dwelling insects.

Previous research has prioritized the largest native sites in the island (i.e. Serra St. Bárbara and Biscoito da Ferraria) for restoration and conservation on the basis that those areas host a high amount of arthropod biodiversity (Borges et al. 2000, 2005; Gaspar et al. 2011). In fact, it has been suggested that exotic forests and semi-natural grassland could also act as corridors for the dispersal of some endemic and native species (Cardoso et al. 2009). However, we show that such areas are unlikely to provide sufficient functional connectivity for more restrict and specialized species, such *C. a. azoricus* and *T. terrabravensis*. Such specialist species may benefit from the creation of stepping-stones or corridors with a vegetation matrix similar the one found in their habitat, shortening the cost of moving between native vegetation areas (Prevedello and Vieira 2010; Eycott et al. 2012). This enhances the probability of dispersals finding other patches by diminishing the distance and time required by dispersals to travel through non-native matrix, therefore minimizing their exposure to threats (Williams et al. 2005; Niebuhr et al. 2015).

The model may be regarded as over-simplistic, as suggested by the low R^2 values obtained. Adding other components of species' biology, habitat and microclimate data or movement and population dynamics would probably improve the robustness of results, since previous studies

have identified them as factors influencing species movement across the landscape (Avendaño-Mendoza et al. 2005; Arellano et al. 2008; Roslin et al. 2009; Le Gall et al. 2017). However, the scarcity of data on our focal species (and generally for the Azorean arthropod fauna), hampered the parameterization and inclusion of such components in the model. In this way, empirical studies are needed to improve the number and precision of the model's parameters, hence improving the precision of connectivity outcomes.

The resistance parameterization, on the other hand, relied on expert knowledge, and one may argue that the quality of expert-based information may vary substantially depending on personal beliefs and experiences (Martin et al. 2012). However, the expertise of the researchers involved in the inquiry, and particularly PAVB, is based on decades of intensive study and fieldwork in Azorean islands, and they are the researchers with higher knowledge in these species. Hence, we are confident that the information provided is accurate. Moreover, the model validation procedures suggested that our framework was robust, namely when compared with other commonly used algorithms. Regarding land-use change scenarios, they were not accounted as none is available for our study area. Although we acknowledge that land-use change scenarios can drastically influence connectivity and management outcomes (in some cases even more than climate change itself—see Albert et al. 2017), it is not expected that the land-use will change in the near future in the Azorean archipelago, as it has not changed significantly in the past decade (Gonçalves and Dentinho 2007).

In conclusion, we showed that our modeling framework can be a useful tool for decision-making process, as it can be easily adapted to generate scenarios of conservation and to validate adaptation options, e.g. planned reforestation, leading to a more informed and useful discussion among stakeholders (Allen et al. 2016).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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