Volcanic caves: priorities for conserving the Azorean endemic troglobiont species

Paulo A.V. Borges 1,2,3∗, Pedro Cardoso1,4,5, Isabel R. Amorim1,2, Fernando Pereira 1,2,3, João P. Constância 2,3, João C. Nunes2,3,6, Paulo Barcelos2,3, Paulino Costa2,3,7, Rosalina Gabriel1, and Maria de Lurdes Dapkevicius8

Abstract:

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Azorean lava-tubes and volcanic pits adequately sampled for arthropod fauna were evaluated for species diversity and rarity. An iterative partial multiple regression analysis was performed to produce a multi-criteria index (Importance Value for Cave Conservation, IV-CC) incorporating arthropod species diversity indices but also including indices qualifying cave geological and management features (e.g., the diversity of geological structures, threats, accessibility). Additionally, we calculated complementarity solutions (irreplaceability and Fraction-of-Spare measures) for each cave with different targets per species, i.e., the minimum number of caves needed for each species to be represented either once or twice. Our results clearly show that to preserve all troglobiont arthropods endemic to the Azores, it is crucial to protect several caves per island. As many as 10 and 15 caves are needed to include one or two occurrences, respectively, per species.

Keywords: multi-criteria index; complementarity; irreplaceability; fraction-of-spare; conservation; Azorean lava-tubes

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INTRODUCTION

Obligate cave-adapted terrestrial species (troglobionts sensu Sket, 2008) tend to exhibit a high degree of endemism, occurring in only one or very few sites (caves) (Barr & Holsinger, 1985; Christman et al., 2005; Culver & Pipan, 2009). This characteristic is particularly important in oceanic archipelagos, in which most troglobionts occur on only one island and are thus Single-Island Endemics (SIEs). Thus, cave-adapted species could be considered very restricted in distribution due to their low dispersal abilities and cave isolation (Christman & Culver, 2001). Cave arthropod diversity can be correlated with habitat availability, i.e., the number of caves, at both local and regional scales (Christman & Culver, 2001) and with the area of the caves (Silva et al., 2011). Moreover, due to the small range size of troglobiont species, alpha local diversity is usually small and partly explained by regional factors (Christman & Culver, 2001; Christman et al., 2005; Malard et al., 2009). Although the area of a cave has been some times correlated with cave diversity (e.g. Silva et al., 2011), the local-regional species richness relationship (i.e., proportional sampling model vs. local saturation model sensu Ricklefs, 1987) has not been formally examined for terrestrial subterranean fauna. Malard et al. (2009) showed that the species richness of stygobionts (aquatic cave-obligate species) in karstic local communities increased linearly with regional richness, whereas that of porous local communities reached an asymptote beyond a certain value of regional richness.

The Macaronesian islands (Azores, Madeira, Selvagens, Canaries, Cape Verde) are of volcanic origin and have hundreds of volcanic caves (i.e., lava-
tubes and volcanic pits) (Borges & Oromí, 1994; Oromí & Izquierdo, 1994). Many species of troglobionts have been described over the past decades for the Macaronesian archipelagos of Madeira (Serrano & Borges, 2010), the Azores (Borges & Oromí, 1994) and the Canaries (Oromí & Martin, 1992; Oromí & Izquierdo, 1994; Oromí, 2004). In the latter two archipelagos, troglobionts represent an important fraction of the unique endemic fauna of the islands (Oromí & Izquierdo, 1994; Oromí, 2004).

In this work, we focus on the arthropod cave-adapted fauna of the Azores. This fauna is in urgent need of conservation because most caves are located in highly disturbed areas, the result of almost 600 years of anthropogenic disturbance and land-use changes in the archipelago (Borges et al., 2009). Because conservation resources are limited, it is impossible to protect all caves inhabited by troglobionts in the Azores. To establish a sound conservation plan, conservation priorities must be set for Azorean caves (Borges et al., 2008). Endangered cave arthropods in the Azores, as elsewhere, are often not considered in national or international conservation policies (Amorim, 2005; Whitten, 2009; Cardoso, 2011; Cardoso et al., 2011a, b). An exception to this lack of attention is the recent list of the top 100 management priority species for the European archipelagos of the Macaronesian region (Martin et al., 2010), which includes several cave-adapted species. However, many cave arthropods are not included in the abovementioned list, namely, species exclusive to caves that are outside officially protected areas. As troglobionts are often the only representatives of a particular trophic guild in a cave, the “health” of a cave ecosystem relies heavily on their existence (Culver & Pipan, 2009).

In a preliminary assessment, Borges et al. (2008) showed that a small number of Azorean volcanic caves are irreplaceable and need to be preserved to protect the current species richness of Azorean troglobionts. Irreplaceability in a conservation planning exercise was originally defined by Pressey et al. (1994) as the frequency of selection of a given site by possible alternative solutions that reach the defined conservation targets. However, as recognized by those authors, this definition had the problem of redundancy. Even sites that were not crucial for achieving the target would be assigned a certain irreplaceability value. Ferrier et al. (2000) then refined the measure by defining irreplaceability as the frequency at which a given site would need to be selected (i.e., would be crucial) in possible alternative solutions to ensure that the conservation targets are achieved. Fraction-of-Spare is a newly developed conservation measure (Phillips et al., 2010) that,

Fig. 1. The Azorean islands, showing the maximum subaerial age in millions of years (Ma) (Nunes, 1999), the number of caves (left of slash) and the number of troglobiont species (right of slash). The Western, Central and Eastern island groups are drawn within separate boxes in the figure and are not shown in their true geographical positions.
like irreplaceability, represents the importance of a site in reaching defined targets or, conversely, specifies the proportion of the available options for reaching the targets that would be lost if a given site was excluded from selection for conservation. The purposes of irreplaceability and Fraction-of-Spare are similar. However, under certain circumstances the Fraction-of-Spare measure may offer advantages that irreplaceability does not provide (see Phillips et al., 2010).

We use data obtained in standardized studies (same sampling effort to all caves) performed during the past two years (2009-2010) to examine the relative value of a set of well-sampled lava tubes and volcanic pits to improve the conservation of the biodiversity of Azorean cave-adapted arthropods. The objectives of this paper are: (i) to test the effectiveness of two widespread ecological patterns, the species-area curve and the relationship between local and regional species richness, in explaining the local diversity of troglobiont species; (ii) to rank caves using a set of criteria such as arthropod diversity- and rarity-based indices as well as cave geological and management features; and (iii) to calculate the irreplaceability and Fraction-of-Spare measures for each cave with different targets per species, i.e., the minimum number of caves needed for each species to be represented either once or twice.

MATERIALS AND METHODS

Sites and data
This study was conducted in the Azores, a volcanic Northern Atlantic archipelago that comprises nine islands distributed from northwest to southeast, roughly between 37° and 40° N and 24° and 31° W. The Azorean islands extend for approximately 615 km and are situated across the Mid-Atlantic Ridge, which separates the western island group (Flores and Corvo) from the central (Faial, Pico, São Jorge, Terceira and Graciosa) and the eastern (São Miguel and Santa Maria) groups (Figure 1). All islands are relatively recent, ranging from 8.12 Myr B.P. (S. Maria) to 250,000 years B.P. (Pico) (Nunes, 1999).

As the result of several recent lava flows in the Azores, many lava-tubes and volcanic pits occur on the islands. A total of 250 cavities were recently listed in a database of the Azorean caves (Pereira et al., in prep.); 163 lava-tubes, 37 pits, 12 pit-caves and 38 cavities of other types (e.g., cavities formed by erosion, artificial caves).

In this study, a total of 42 volcanic cavities (37 lava-tubes and 5 volcanic pits) on six of the nine Azorean islands (excluding S. Maria, Flores and Corvo) were surveyed and are listed (see Table 1). A number of those caves were surveyed intensively during 1988 and 1990 by two expeditions sponsored by the National Geographic Society under the supervision of Pedro Oromí (Univ. de La Laguna, Spain) and Philippe Ashmole (Univ. of Edinburgh, UK) (see Oromí et al., 1990). However, many of the caves were also sampled by researchers at the University of the Azores and “Os Montanheiros” (see Borges &

| Cave                                | Island     | IV-CC |
|-------------------------------------|------------|-------|
| Furna dos Montanheiros             | Pico       | 0.683 |
| Gruta de Água de Pau               | São Miguel | 0.682 |
| Algar do Morro Pelado              | São Jorge  | 0.594 |
| Gruta do Chocolate                 | Terceira   | 0.582 |
| Gruta das Agulhas                  | Terceira   | 0.582 |
| Gruta dos Balcões                   | Terceira   | 0.563 |
| Gruta do Soldão                     | Pico       | 0.562 |
| Algar das Bocas do Fogo            | São Jorge  | 0.557 |
| Gruta do Henrique Maciel           | Pico       | 0.549 |
| Furna das Cabras II (terra)        | Pico       | 0.539 |
| Algar do Carvão                    | Terceira   | 0.530 |
| Gruta da Ribeira do Fundo          | Pico       | 0.527 |
| Gruta do Coelho                    | Terceira   | 0.491 |
| Gruta de Santa Maria               | Terceira   | 0.489 |
| Gruta da Branca Opala              | Terceira   | 0.485 |
| Furna Nova I                        | Pico       | 0.482 |
| Gruta da Malha                      | Terceira   | 0.478 |
| Gruta das Torres                    | Pico       | 0.469 |
| Furna do Enxofre                   | Graciosa   | 0.468 |
| Gruta da Achada                    | Terceira   | 0.468 |
| Gruta do Pico da Cruz              | São Miguel | 0.467 |
| Gruta do Carvão                     | São Miguel | 0.460 |
| Furna de Frei Matias               | Pico       | 0.458 |
| Gruta da Agostinha                 | Pico       | 0.455 |
| Gruta da Madre de Deus             | Terceira   | 0.454 |
| Gruta do Mistério da Silveira I    | Pico       | 0.453 |
| Gruta do Pico Queimado             | São Miguel | 0.453 |
| Gruta das Canárias                 | Pico       | 0.447 |
| Gruta das Anelares                  | Faial      | 0.447 |
| Gruta do Natal                      | Terceira   | 0.444 |
| Gruta do Caldeira                  | Terceira   | 0.439 |
| Gruta da Beira                      | São Jorge  | 0.437 |
| Gruta do Cabeço do Canto            | Faial      | 0.407 |
| Furna da Baliza                     | Pico       | 0.404 |
| Gruta dos Principiantes            | Terceira   | 0.401 |
| Gruta do Enforcado                 | São Miguel | 0.396 |
| Gruta dos Buracos                   | Terceira   | 0.392 |
| Gruta do Esqueleto                 | São Miguel | 0.380 |
| Gruta dos Vimes                     | Pico       | 0.371 |
| Galeria do Forninho                 | Graciosa   | 0.367 |
| Furna Ruim                          | Faial      | 0.366 |
| Gruta do Parque do Capelo           | Faial      | 0.359 |
Oromi, 1994) and in more recent studies (e.g., Borges et al., 2004, 2007; Amorim, 2005). The cave arthropod presence/absence data are in part unpublished and resulted from recent surveys performed by Isabel Amorim and Fernando Pereira (2009 and 2010) and by Paulo Borges and Fernando Pereira within the FCT project PTDC/AMB/70801/2006 - Understanding Underground Biodiversity: Studies of Azorean Lava Tubes (2009-2011). In this study we only include caves which were subject to comparable standardized protocols: all caves were surveyed using baited pitfalls and also standardized time search methods covering the deep zone of complete darkness, the transition zone of near-complete darkness, the twilight zone near the cave entrance and the cave entrances (see more details in Oromi et al., 1990).

**Data analysis**

Based on the recent Borges et al. (2010) list of Azorean arthropods, the species were classified in one of three colonization categories: endemics (species occurring only in the Azores, as a result of either speciation events (neo-endemics) or extinction of the mainland populations (palaeo-endemics)), natives (i.e. species which arrived by long-distance dispersal in the Azores and which also occur in other archipelagos and/or on continents) and introduced (i.e. species believed to occur in the archipelago as a result of human activities; some of these species have a worldwide distribution). In doubtful cases, a species was assumed to be native. Moreover, based on the species traits cited in Borges & Oromi (1994) and Reboleira et al. (2011), the species were also classified as follows (Skt, 2008): troglobionts - species adapted to the cave environment and generally unable to survive in epigean environments; eutroglophiles - species that can spend their entire lives in caves but occur in other environments; subtroglophiles - species that use caves but cannot complete their life cycle in caves; and trogloxenes - species occurring sporadically in caves and unable to establish a subterranean population.

In the current paper, we use primarily the troglobiont and eutroglophile Azorean endemic species for further analyses. Ordinary regression methods were used to relate species diversity to cave length (a surrogate of true cave area) and local (cave) and regional (island) species richness. Local species richness was calculated as the mean number of species per cave in a particular island and regional species richness is the total number of species known from each island (see Srivastava, 1999).

To prioritize the 42 volcanic caves, two techniques were used: i) indices for scoring conservation priorities based on comparative analyses; and ii) methods based on the complementarity of sites and their contribution toward given targets.

**Scoring method**

Due to its simplicity, a scoring approach involving a multi-criteria index based on nine different indicators was used. This approach incorporated biological information and also included cave geological and management features. The partial indicators corresponding to the selected biological characteristics included the following measures: the species richness of troglobiont arthropods (Strogl), selected because reflects the presence of unique specialized fauna; the species richness of Azorean endemic arthropods (including troglobionts, eutroglophiles, subtroglophiles and trogloxenes) (Send), selected because reflects the presence of unique evolutionary Azorean diversity; and the number of rare species (here equivalent to SIEs) (Srare), selected because gives some value to caves with species with very restricted distribution.

The partial indicators corresponding to the selected cave characteristics (data from IPEA database, Constância et al., 2004; Borges et al., 2008) (see Appendix 1 for more details) were selected to cover features of the caves representing their geology, threats and management: show cave (Show), that is based of a combination of cave size and diversity of scenic structures; geology (GEO), that is based on the number and uniqueness of speleothems and other geological structures; the difficulty of exploration (Dif. Expl.), that is based on a gradient of cave progression by visitors; integrity (Integrity), that is based on the pristine state of the cave; the anthropogenic threats index (Threats), that is based in a gradient of human disturbance in the epigean habitats; and accessibility (Access), that is based on how easily is the cave accessible to people.

**Multi-criteria index: Importance Value for Cave Conservation (IV-CC)**

If different criteria are combined to construct a single index, it is difficult to define what the single value represents (see Borges et al., 2005). Moreover, the different indices used to describe a cave value may be related. This similarity may cause a given feature to receive a higher weighting in the construction of the complex index. To avoid possible problems of collinearity, we have used partial regression analysis techniques (Legendre & Legendre, 1998, see also Borges et al., 2005), which allow the separation of the variability of a given predictor that is independent of (i.e., not related to) the variability of another variable or set of variables. For this purpose, we applied generalized linear models (GLM) with natural logarithm link functions. In these models, the independent predictor is regressed against the potentially non-independent variable or group of variables, and the resulting residuals are retained as the independent term representing the variable. In this particular case, we have developed iterative partial regression analyses in which each iteration extracts the variability of a predictor that is independent of the formerly chosen indices. After selecting a first index (A), which is used without any transformation in the Importance Value for Cave Conservation (IV-CC) calculations, we regressed the second index (B) against A, obtaining its residuals (rB). In successive steps, each index (e.g., C) is regressed against the previously included quantities (in this case, A and rB) in a multiple regression analysis to obtain its residuals (rC). The first selected index to be used without any transformation was the total number of cave-adapted endemic species (S\textsubscript{trog.}) because cave-adapted species...
richness was considered of major importance to cave conservation. The other indices were entered in the model according to the decreasing order of their $r^2$ values resulting from a GLM regression of each index with $S_{trog}$. Thus, the final IV-CC is as follows:

$$IV-CC = \left(\frac{S_{trog}}{S_{trog}_{max}} + \frac{R_{Show}}{R_{Show}_{max}} + \frac{R_{Integrity}}{R_{Integrity}_{max}} + \frac{R_{Threats}}{R_{Threats}_{max}} + \frac{R_{1/Dif.Expl.}}{R_{1/Dif.Expl.}_{max}} + \frac{R_{1/Access}}{R_{1/Access}_{max}}\right) / 9.$$

In this index, the value of the residual variance ($R$) of each of the additional indices for a given cave is divided by the maximum value ($max$) obtained within all caves. For instance, the residuals of “Show” were obtained from the polynomial model $Show = a + b S_{trog} + c R_{End}$. We used the inverses of the indices Dif.Expl. and Access because the way in which these indices were originally built is counterintuitive. The IV-CC composite index has a maximum value of 1 (see also Borges et al., 2005).

**Complementarity**

An algorithm coded in Java software (available from P. Cardoso; see also Gaspar et al., 2011 for another implementation) was used to calculate the irreplaceability of each cave. We first defined targets for two different analyses by requiring that either one or two caves where a particular species occurs be represented in the datasets obtained from the analysis. The algorithm begins with a dataset including all of the caves studied. Based on the targets to be achieved, the algorithm attempts to exclude caves from this dataset at random. The selected cave is excluded from the dataset if its exclusion can occur without compromising the species targets. A new cycle with a dataset consisting of the remaining caves then begins. However, if the selected cave cannot be excluded, another cave is randomly excluded and the new dataset evaluated. This procedure was repeated until the exclusion of any cave from the dataset would prevent the species targets from being achieved. A minimum set of caves is not the only dataset determined by the algorithm. The program will also determine alternative solutions with higher numbers of caves if all of the caves selected are absolutely required to achieve the desired targets. These alternative outcomes furnish the flexibility that solutions should possess. A site found to be important but difficult or costly to preserve in a minimum solution may be replaced with two other sites in a larger solution. The program performs 10,000 iterations. From the alternative solutions found, it calculates the percentage of times that a site was selected. This percentage is the irreplaceability value for that site. The value ranges from 0 (the site is redundant in all cases) to 100 (the site is absolutely irreplaceable).

We also calculated another complementarity algorithm, the Fraction-of-Spare (Phillips et al., 2010) for all studied caves using the same targets: all troglobiont species must occur in either one or two
caves. This measure was calculated as a complement to irreplaceability as, even if the objectives are the same, it may present some advantages (Phillips et al., 2010). By assigning value to every site with some feature of conservation importance it does not undervalue many of such sites as usually occurs with the irrereplaceability measure. It presents the additional advantage of being much less computationally intensive compared to irrereplaceability, an important characteristic when dealing with large datasets. Although both summed and maximum Fraction-of-Spare may be used for conservation priorities, we used the latter so that caves with few but unique species would be highly ranked.

As stated above, the irrereplaceability analyses were based on datasets for which no site could be excluded without compromising the targets. A minimum number of caves were selected in many of these datasets. Taking advantage of such algorithm, we also calculated the minimum number of sites needed to reach the different targets and determined the combinations of sites that allowed any minimum set to be reached.

RESULTS

We recorded 49 species of endemic arthropods in the 42 caves (see Appendix 2). Of these species, 17 (35%) are troglobionts, 18 (37%) eutroglophiles. Most troglobiont endemic species occur in few caves: a total of 61% of these species occur in at most three caves (Fig. 2). Six species are particularly widespread. The pseudoscorpion Pseudoblothrus vulcanus occurred in eight caves, the spider Rugathodes pico in seven, the centipede Lithobius obscurus azoreae in 12, the cave root-hopper Cixius azopicavus in six and the ground-beetles Trechus picoensis and T. terceiranus in eight and ten caves, respectively.

No troglobiont species were recorded in six of the caves studied. One cave has four troglobiont species (Furna dos Montanheiros, Pico island), eight have three species, 13 caves have two species and 14 caves have one species. Furna dos Montanheiros (Pico island) has eight endemic troglobionts or eutroglophiles, and five additional caves have at least six troglobiont or eutroglophile species (Gruta da Agostinha, Gruta do Henrique Maciel and Gruta do Soldão on Pico island, Gruta das Agulhas and Gruta do Coelho on Terceira island).

Cave length is a predictor of troglobiont species richness (model: log (S+1) = 0.12 + 0.13 log Area; r² = 0.33; p = 0.0007) (Fig. 3).

The mean local endemic troglobiont cave species richness (alpha diversity) is a linear function of the regional number of species (gamma diversity) is a linear function of the importance of cave length (as a surrogate of cave area) as a predictor of species diversity, which was rarely observed in cave studies (but see Silva et al., 2011). The low r² observed is due to the fact that other variables not taken into account in this study are also explaining the observed number of species. Islands with more troglobiont and eutroglophile species tend to have more species per cave on average. This result
Table 2. Irreplaceability, fraction of spare and caves included in the minimum datasets with two different targets: troglobiont species represented in at least one or two caves. For the minimum datasets, X represents caves that are part of all minimum datasets and other letters represent groups of caves that may be replaced by each other; numbers after letters represent how many caves must be included from the group so that the minimum dataset is reached.

| Site                              | Island  | Target 1 | Target 2 | Target 1 | Target 2 | Target 1 | Target 2 |
|-----------------------------------|---------|----------|----------|----------|----------|----------|----------|
| Gruta do Parque do Capelo         | Faial   | 1        | 1        | 1        | 1        | X        | X        |
| Algar das Bocas do Fogo           | São Jorge | 1      | 1        | 1        | 1        | X        | X        |
| Algar do Morro Pelado             | São Jorge | 1      | 1        | 1        | 1        | X        | X        |
| Gruta da Beira                    | São Jorge | 1      | 1        | 1        | 1        | X        | X        |
| Gruta de Água de Pau              | São Miguel | 1      | 1        | 1        | 1        | X        | X        |
| Gruta das Aguihas                 | Terceira | 1       | 1        | 1        | 1        | X        | X        |
| Gruta das Anelares                | Faial   | 0.5075   | 1        | 1        | 1        | A(1)     | X        |
| Furnas das Cabras II (terra)      | Pico    | 0.5044   | 1        | 1        | 1        | B(1)     | X        |
| Gruta da Ribeira do Fundo         | Pico    | 0.4956   | 0.7023   | 0.5      | 1        | X        | X        |
| Gruta do Cabeço do Canto          | Faial   | 0.4925   | 1        | 1        | 1        | A(1)     | X        |
| Fuma dos Montanheiros             | Pico    | 0.3794   | 0.7023   | 0.5      | 1        | X        | X        |
| Algar do Carvão                   | Terceira | 0.3381  | 0.6674   | 0.5      | 1        | C(1)     | A(2)     |
| Gruta de Santa Maria              | Terceira | 0.3361  | 0.6653   | 0.5      | 1        | C(1)     | A(2)     |
| Gruta da Malha                    | Terceira | 0.3256  | 0.6673   | 0.5      | 1        | C(1)     | A(2)     |
| Gruta dos Vimes                   | Pico    | 0.3117   | 0.6491   | 0.5      | 1        | B(1)     |          |
| Fuma de Frei Matias               | Pico    | 0.3089   | 0.6486   | 0.5      | 1        | B(1)     |          |
| Gruta da Agostinha                | Pico    | 0.1536   | 0.2876   | 0.2      | 0.25     | C(1)     |          |
| Gruta do Soldão                   | Pico    | 0.1532   | 0.2926   | 0.2      | 0.25     | C(1)     |          |
| Gruta do Mistério da Silveira I   | Pico    | 0.1383   | 0.278    | 0.2      | 0.25     | C(1)     |          |
| Gruta das Canárias                | Pico    | 0.1364   | 0.2778   | 0.2      | 0.25     | C(1)     |          |
| Gruta das Torres                  | Pico    | 0.0601   | 0.1617   | 0.2      | 0.25     |          |          |
| Fuma Ruim                         | Faial   | 0.054    | 0.0941   | 0.166667 | 0.2      |          |          |
| Gruta do Henrique Maciel          | Pico    | 0.0511   | 0.0888   | 0.166667 | 0.2      |          |          |
| Gruta dos Balcões                 | Terceira | 0.0252  | 0.0128   | 0.111111 | 0.125    |          |          |
| Galeria do Forninho               | Graciosa | 0.0249  | 0.0156   | 0.090909 | 0.1      |          |          |
| Gruta dos Buracos                 | Terceira | 0.0243  | 0.0139   | 0.090909 | 0.1      |          |          |
| Gruta da Branca Opala             | Terceira | 0.0229  | 0.0173   | 0.090909 | 0.1      |          |          |
| Gruta da Achada                   | Terceira | 0.0224  | 0.016    | 0.111111 | 0.125    |          |          |
| Gruta da Madre de Deus            | Terceira | 0.0223  | 0.0151   | 0.090909 | 0.1      |          |          |
| Fuma da Baliza                    | Pico    | 0        | 0        | 0.142857 | 0.166667 |          |          |
| Furna Nova I                      | Pico    | 0        | 0        | 0.142857 | 0.166667 |          |          |
| Gruta do Caldeira                 | Terceira | 0        | 0        | 0.111111 | 0.125    |          |          |
| Gruta do Chocolate                | Terceira | 0        | 0        | 0.111111 | 0.125    |          |          |
| Gruta do Coelho                   | Terceira | 0        | 0        | 0.142857 | 0.166667 |          |          |
| Gruta do Natal                    | Terceira | 0        | 0        | 0.111111 | 0.125    |          |          |
| Gruta dos Principiantes           | Terceira | 0        | 0        | 0.142857 | 0.166667 |          |          |
implies that there is no signal of local community saturation of species at the cave scale and that overall island regional diversity is an effective predictor of local cave diversity. Moreover, our results confirm the predictions of empirical studies suggesting that the size of most local cave species assemblages is proportional to the size of the regional pool of potential colonists (Malard et al., 2009; see review for epigean fauna in Srivastava, 1999).

The current study is novel because we combined cave biological, geological and management characteristics in a multi-criteria index, the Importance Value for Cave Conservation (IV-CC) composite index first proposed by Borges et al. (2005) for epigean forest arthropods using only biological data. The strategy followed allows biological data to be combined with geodiversity and other cave information to better predict the conservation value of caves. The results obtained indicate that the caves of Terceira and Pico islands may be considered conservation hotspots at the scale of the Azores. These islands also have the greatest numbers of caves, and most of the efforts at conservation management should therefore be directed at Terceira and Pico islands. However, the restricted distribution of the single-island endemics occurring in the caves of the islands of São Miguel, São Jorge and Faial implies that strict conservation management measures should also be applied to the caves listed in the minimum complementary set of caves (Table 2). In fact, this conservation exercise highlights the importance of São Jorge Island, where all of the caves studied represent the sole habitat for unique single-island endemics, one species per cave (Algar do Morro Pelado, Algar das Bocas do Fogo and Gruta da Beira).

In all, 36 caves have at least one troglobiont species. However, the protection of only 10 caves is needed to conserve the 17 troglobiont species in at least one cave. Eight different combinations of 10 caves constituted the minimum datasets if the target was one representation per species (Table 2). A close look at those caves shows that three highly relevant caves are not included in the top-ranked caves based on the IV-CC. These three caves are Gruta da Beira (São Jorge island), Gruta das Anelares and Gruta do Parque do Capelo (Faial island). These caves are small. The major threats to their conservation include land use changes (pasture intensification) that tend to produce an impermeable cave roof and to compact the cave floor (e.g., Gruta da Beira, S. Jorge island); pollution (e.g., sewage or waste disposal); the introduction of exotic plants and/or animals; and disturbance by human visitation. Unfortunately, these processes also threaten most of the top-ranked caves listed simultaneously in Tables 1 and 2. Human visitation to the show-caves (Algar do Carvão, Gruta do Natal, Furna do Enxofre, Gruta das Torres and Gruta do Carvão) has certain negative impacts, particularly in Algar do Carvão and Gruta do Carvão, which have long periods of visitation during the year. In Algar do Carvão, the intensive show-cave activity is markedly impacting the temperature and relative humidity of the cave. These changes have already produced visual impacts through the spread of green algae in the speleothems (see http://gigapan.org/gigapans/83300/) and the decreasing activity density of the ground-beetle Trechus terceiranus as measured using replacement-trapping techniques (Cardoso et al., subm.; P.A.V. Borges et al., unpublished data). The case of Gruta das Torres (Pico island) is less problematic because only a small part of the cave is open to the public and visitors use only portable lights.

Interestingly, the minimum dataset of caves needed to conserve the 17 troglobiont species at least once (target 1) (Table 2) does not include certain caves whose numbers of troglobionts and eutroglophiles make the caves biodiversity hotspots: Gruta do Henrique Maciel (Pico island) and Gruta do Coelho (Terceira island). However, this finding does not mean that these caves have less importance. These caves are needed as members of a network of caves that could adequately reinforce the conservation of cave animals on Terceira and Pico islands. In fact, because many caves are isolated entities they lack the “rescue effect”: only “source” populations can be maintained in ecological and evolutionary time (Rosenzweig, 1995). This disagreement highlights the importance of using complementary information on conservation strategies.

The application of correct management measures urgently requires attention. Certain steps in this direction are already being taken by the Azorean Government through the preparation of new legislation, but willingness of enforcement is another matter all together. In fact, the dynamics and interactive nature of the epigean habitat matrix imply the need for certain precautionary strategies. The economically important pastures that support the production of dairy products generate substantial impacts in the aboveground catchment areas surrounding the caves. Both this factor and tourism will imply a continuous decrease in the quality of Azorean cave ecosystems. With the exception of Algar do Carvão (Borges & Pereira, unpublished data) and certain additional caves in Terceira and Pico (Amorim & Pereira, unpublished data), no monitoring of troglobiont populations is conducted in the Azores. Accordingly, few reliable data will be available for current IUCN red listing strategies (but see Cardoso et al., 2011a).

Important research was performed on Azorean cave biodiversity in the past two decades, but further taxonomic and ecological work is also needed because many unknown species may remain unrecorded and because other overlooked habitats need further investigation (e.g., MSS on older islands). The direct dependency of cave animals on a stable high relative humidity also implies the need for certain mitigation measures in Azorean show-caves.

Although the ranking obtained using IV-CC incorporates a wide range of cave characteristics (biological, geological, management), the inclusion of genetic diversity measures (Amorim, 2005; Amorim et al., unpublished data) may further improve the conservation value of the IV-CC multi-criteria index presented here. Another possibility would be the study of phylogenetic diversity and differentiation between caves. Future research in this area could help to
improve the currently proposed conservation priorities. Overall, given the multi-criteria IV-CC and the robust complementarity measures developed by our study, we strongly propose the use of our methodology to define future cave priority management strategies in the Azores. It is possible that our methodology can also be used elsewhere for this purpose.

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Appendix 1. List of indicators selected to describe geology, threat and management features of the caves (adapted from Constância et al., 2004)

| Code | Indicator               | Explanation                                                                 |
|------|-------------------------|-----------------------------------------------------------------------------|
| Show | Show cave               | 0  No information available                                                 |
|      |                         | 1  Small cave (less than de 100 m length x 2 m height)                      |
|      |                         | 2  Small and simple cave with at least 100 m and less than 200 m            |
|      |                         | 3  Size between 200 and 500 m but few interesting structures               |
|      |                         | 4  Large caves (more than 500 m) and with diversity of structures          |
|      |                         | 5  Very large caves (more than 1000 m) and with diversity of structures    |
| GEO  | Geology                 | 0  No information available                                                 |
|      |                         | 1  Absence of relevant geological structures                               |
|      |                         | 2  Presence of very common geological structures (e.g. lava stalactites)   |
|      |                         | 3  Presence of common geological structures (e.g. benches, striated walls) |
|      |                         | 4  Presence of rare geological structures (e.g. secondary deposits, levees, multiple levels of lava tubes, etc.) |
|      |                         | 5  Presence of very rare geological structures (e.g. gas bubbles, stalagmite, columns) |
| Dif.Expl. | Difficulty of Exploration | 0  No information available                                               |
|      |                         | 1  Lava tube or pit of difficult exploration due to difficulty of progression |
|      |                         | 2  Cavity with some obstacles                                              |
|      |                         | 3  Some obstacles present but easy to transpose                            |
|      |                         | 4  Very easy exploration - all people could visit the cave                 |
| Integrity | Integrity             | 0  No information available                                                 |
|      |                         | 1  More than 50% of the cave destroyed                                     |
|      |                         | 2  Some evidences of destruction (< 50% of the cave’s length)             |
|      |                         | 3  More than 90% of the cave’s length well preserved but Human disturbance |
|      |                         | 4  Well preserved cave and few signs of Human disturbance                  |
|      |                         | 5  Very well cave preserved                                                |
| Threats | Anthropogenic Threat | 0  No information available                                                 |
|      |                         | 1  Partially destroyed cave due to epigean Human disturbance               |
|      |                         | 2  Identified epigean Human activities that could cause near-future disturbance |
|      |                         | 3  Identified epigean Human activities that could cause future disturbance |
|      |                         | 4  Identified epigean Human activities that present no potential threat    |
|      |                         | 5  No Human activities or threats in the area of the cave                 |
| Access | Accessibility          | 0  No information available                                                 |
|      |                         | 1  Very difficult to access - no roads or tracks available                 |
|      |                         | 2  Difficult access - no near locality and more than 45 m walk            |
|      |                         | 3  Difficult access - no near locality or property owner needs to grant access |
|      |                         | 4  Easy access, with available public transport                            |
|      |                         | 5  Easy access, easy to locate, near a locality                            |
Appendix 2. List of endemic arthropods present in the 42 caves of the Azores. Adaptation: T - troglobionts; E - eutroglophiles; S - subtroglophiles; Tr - trogloxenes.

| Classe        | Order        | Family       | Species                                                                 | Adaptation |
|---------------|--------------|--------------|-------------------------------------------------------------------------|------------|
| Arachnida     | Pseudoscorpiones | Syarinidae  | Microcreagrella caeca caeca (Simon, 1883)                               | E          |
| Arachnida     | Pseudoscorpiones | Syarinidae  | Pseudoblothrus oromii Mahnert, 1990                                    | T          |
| Arachnida     | Pseudoscorpiones | Syarinidae  | Pseudoblothrus vulcanus Mahnert, 1990                                   | T          |
| Arachnida     | Oribatida     | Cepheidae    | Tritteus (n. sp.) Morell & Subias                                      | E          |
| Arachnida     | Oribatida     | Damaeidae    | Damaeus pomboi Pérez-Iñigo, 1987                                       | E          |
| Arachnida     | Oribatida     | Galumnidae   | Galumna sp. (n. sp.) Morell & Subias                                   | E          |
| Arachnida     | Oribatida     | Liacaridae   | Liacarus angustatus (Weigmann, 1976)                                   | E          |
| Arachnida     | Oribatida     | Nothridae    | Nothrus palustris azorensis Pérez-Iñigo, 1897                          | E          |
| Arachnida     | Oribatida     | Phthiracaridae | Phthiracarus falciformis Morell & Subias, 1991             | E          |
| Arachnida     | Araneae       | Araneidae    | Gibbaranea occidentalis Wunderlich, 1989                                | S          |
| Arachnida     | Araneae       | Linyphiidae  | Leptephyantes acoreensis Wunderlich, 1992                               | S          |
| Arachnida     | Araneae       | Linyphiidae  | Porrhomma borgesi Wunderlich, 2008                                      | E          |
| Arachnida     | Araneae       | Linyphiidae  | Tuninyphia cavernicola Wunderlich, 2008                                 | T          |
| Arachnida     | Araneae       | Lycosidae    | Pardosa acorensis Simon, 1883                                           | T          |
| Arachnida     | Araneae       | Theridiidae  | Rugathodes acorensis Wunderlich, 1992                                   | S          |
| Malacostraca  | Amphipoda     | Talitridae   | Macarorchestia martini Stock, 1989                                     | T          |
| Malacostraca  | Amphipoda     | Talitridae   | Orchestia chevreuxi De Guerne, 1887                                    | S          |
| Malacostraca  | Isopoda       | Philosciidae | Chaetophiloscia guernei (Dolffus, 1887)                                 | E          |
| Malacostraca  | Isopoda       | Trichoniscidae | Gen. nov. sp. nov.                                                     | T          |
| Chilopoda     | Lithobiomorpha | Lithobidae   | Lithobius melanops borgei Eason & Ashmole, 1992                         | T          |
| Chilopoda     | Lithobiomorpha | Lithobidae   | Lithobius obscurus azoreae Eason & Ashmole, 1992                        | T          |
| Collembola    | Poduromorpha  | Onychiuridae | Onychiurus n. sp. Gama                                                  | E          |
| Collembola    | Entomobryomorpha | Entomobryidae | Pseudosinella ashmoleorum Gama, 1988                                   | E          |
| Collembola    | Entomobryomorpha | Entomobryidae | Pseudosinella azorica Gama, 1988                                       | E          |
| Insecta       | Hemiptera     | Cixiidae     | Cixius azopicavus Hoch, 1991                                            | T          |
| Insecta       | Hemiptera     | Cixiidae     | Cixius azopifajo azopifajo Remane & Asche, 1979                         | S          |
| Insecta       | Hemiptera     | Cixiidae     | Cixius azoterceirae Remane & Asche, 1979                                | S          |
| Insecta       | Hemiptera     | Cixiidae     | Cixius cavazoricus Hoch, 1991                                           | T          |
| Insecta       | Coleoptera    | Carabidae    | Bembidion schmidti mequignon Colas, 1939                                | Tr         |
| Insecta       | Coleoptera    | Carabidae    | Thalassophilus azoricus Oromi & Borges, 1991                            | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus isabelae Borges & Serrano, 2007                                 | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus jorgensis Oromi & Borges, 1991                                  | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus montanheiroorum Oromi & Borges, 1991                            | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus oromii Borges, Serrano & Amorim, 2004                           | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus pereirai Borges, Serrano & Amorim, 2004                         | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus picoensis Machado, 1988                                         | T          |
| Insecta       | Coleoptera    | Carabidae    | Trechus terceiranus Machado, 1988                                       | T          |
| Insecta       | Coleoptera    | Curculionidae | Drouetius azoricus Drouet, 1859                                         | Tr         |
| Insecta       | Coleoptera    | Curculionidae | Drouetius borgesi centralis Machado, 2009                              | Tr         |
| Insecta       | Coleoptera    | Dystiscidae  | Hydroporus guernei Réginhardt, 1891                                    | Tr         |
| Insecta       | Coleoptera    | Zopheridae   | Tarphius tornvall Gillerfors, 1985                                      | Tr         |
| Insecta       | Lepidoptera   | Yponomeutida | Argynesthesia atlanticella Rebel, 1940                                  | Tr         |
| Insecta       | Diptera       | Phoridae     | Megaselia leptoferm Disney, 2007                                        | E          |
| Insecta       | Diptera       | Phoridae     | Megaselia miquelensis Disney, 2007                                      | E          |