Do richness and rarity hotspots really matter for orchid conservation in light of anticipated habitat loss?

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ABSTRACT

Aim The aim of this analysis was to identify strategies that will maximize efficiency and effectiveness in conservation planning. As many orchids are threatened with extinction for various reasons, our primary objective was to combine hotspots analyses with stochastic extinction modelling to highlight possible conservation priorities for Lepanthes spp. (Orchidaceae) based on patterns of richness, rarity and threat. Our subsequent objective was to identify potential conservation surrogates and variables that are the best predictors of extinction probabilities. The ultimate goal was to determine which factors should be emphasized in conservation planning to prevent species extinctions.

Location Latin America; the Caribbean.

Methods We used herbarium records and ArcGIS to map the distribution of Lepanthes spp. and to identify hotspots of richness and rarity. We forecasted extinction patterns with Koopowitz’s stochastic extinction model and calculated extinction probabilities in each country. We used a randomForest regression model in R to assess the importance of richness, rarity and threat for explaining extinction probabilities.

Results Hotspots of Lepanthes richness and rarity occurred in north-western South America and southern Central America and largely overlapped with each other. The highest extinction probabilities occurred in northern Central America, Haiti and Ecuador, and generally, hotspots of richness and rarity did not correspond with patterns of threat. Habitat loss was the most important variable for explaining extinction probabilities, followed by measures of rarity.

Main conclusions Conservation efforts will be most efficient in richness and rarity hotspots, and because they overlap, rarity hotspots could act as surrogates for protecting overall Lepanthes diversity. Hotspots rarely occurred in the most threatened areas, and therefore, conservation efforts are more urgent in non-hotspot areas. Conservation efforts will be most effective if they combine ex situ strategies in locations with high habitat conversion rates with reservation strategies in rarity and richness hotspots, particularly where they overlap.

Keywords Biodiversity hotspots, deforestation rates, Lepanthes (Orchidaceae), random forest models, rare plants, stochastic extinction models.
INTRODUCTION

Habitat loss continually threatens the Earth’s biodiversity, and identifying conservation priority areas for research, management and preservation is a substantial challenge for biologists, managers and policy makers in charge of preventing biodiversity loss (Brooks et al., 2002; Whittaker et al., 2007; Gillespie et al., 2012; Joppa et al., 2013). Understanding species’ geographic distributions and patterns of the threats they face is essential for proactively addressing this challenge as it allows planners to forecast extinctions and to identify priority areas for conservation (Koopowitz et al., 1994; Gaston, 1996; Abbitt et al., 2000; Gaston & Fuller, 2009). The process of identifying conservation priority areas is complicated by the fact that not all species groups or biotas have comparable distributions and they are not all equally sensitive to threats (Prendergast et al., 1993; Koopowitz et al., 1994; Kerr, 1997; Brooks et al., 2006). Consequently, appropriate priority areas may vary considerably according to the location or the taxonomic group of concern (Prendergast et al., 1993; Kerr, 1997; Stork, 2010). Therefore, patterns of richness, threat and vulnerability need to be established for additional representative groups so that conservation priority areas can be refined. Moreover, additional analyses will help to clarify whether particular groups of organisms or specific areas can act as effective surrogates for protection of biodiversity in general.

Focusing on centres of species richness, that is, biodiversity hotspots, has been widely acknowledged as an efficient global conservation strategy (Myers et al., 2000; Myers, 2003; Brooks et al., 2006; Joppa et al., 2013). Mapping and analysing the distribution of hotspots has proven fruitful for focusing conservation efforts and has resulted in improved protection for an array of organisms in many locations (e.g. Williams et al., 1996; Hooper et al., 2002; Roberts et al., 2002; Müller et al., 2003; Gjerve et al., 2004). Additionally, because many of the world’s undocumented species likely occur in biodiversity hotspots (Joppa et al., 2011; Scheffers et al., 2012), protecting these locations could prove to be an effective conservation strategy even amidst data limitations. Thus, it is not surprising that hotspot conservation is a highly acclaimed strategy among conservation practitioners (Myers, 2003).

Nevertheless, several studies have questioned the value of focusing on biodiversity hotspots as conflicting results often arise when comparing multiple organisinal groups (Prendergast et al., 1993; Grenyer et al., 2006; Kohlmann et al., 2010), common versus rare species (Prendergast et al., 1993; Williams et al., 1996; Bonn et al., 2002; Orme et al., 2005), and differing scales of analysis (Reid, 1998; Gjerde et al., 2004). In an analysis of several taxonomic groups ranging from birds to liverworts, Prendergast et al. (1993) concluded that many richness hotspots are not effective conservation surrogates for rare or restricted species. Additionally, it has been argued that overly emphasizing conservation of biodiversity hotspots (i.e. high species numbers) leads to neglect of other significant areas or ecosystems that may have unique biological, environmental or cultural value (Kareiva & Marvier, 2003). Accordingly, complementarity, or maximizing the number of unique species in a minimal area, is an important consideration for effective conservation planning (Williams et al., 1996; Reyers et al., 2000). Furthermore, many hotspots analyses do not incorporate threats into their models, and researchers have shown that centres of species richness may not correspond with patterns of threat (Orme et al., 2005), rendering them markedly less important conservation priorities.

Incorporating vulnerability in conservation planning is critical for success (Wilson et al., 2005), and models have been developed that are useful for predicting where species are likely to succumb to threats such as habitat loss (e.g. Koopowitz, 1992; Koopowitz et al., 1994). Koopowitz (1992) developed a stochastic extinction model that makes use of readily available species distribution data and deforestation trends to model extinction patterns for several plant groups (Koopowitz et al., 1993, 1994). Although the model is based on several underlying assumptions (see Appendix S1 in Supporting Information), it is practical and it generates results that match well with the predictions of other extinction models (e.g. species–area curves; Dial, 1995). Therefore, by applying this model to distinct geographic areas, extinction estimates can be calculated for specific locations across the global landscape as a means of incorporating threat and vulnerability into the process of identifying conservation priority areas (Koopowitz, 1992; Wilson et al., 2005).

Accordingly, our objective was to combine hotspots analyses and stochastic extinction modelling to identify potential conservation priority areas. Comparisons could then be made between species groups, and between patterns of richness, rarity and threat. Because tropical orchids are among the most endangered groups on the planet given their often limited spatial distributions and specific ecological interactions (Koopowitz, 1992; Tremblay, 1997; Pitman & Jørgensen, 2002; Swarts & Dixon, 2009; Oldfield, 2010; Seaton et al., 2013) and because they have yet to be emphasized in hotspots analyses, we tested this combination of analyses on a species rich group of orchids that is threatened throughout much of its range, Lepanthes Sw. (Orchidaceae Juss.). We had three specific aims: 1) map the distribution of Lepanthes species and rarity richness patterns to identify hotspots, that is, centres of richness, and evaluate the degree to which these features overlap; 2) forecast patterns of extinction for Lepanthes spp. and assess whether hotspots of species and rarity richness correspond with high extinction probabilities; and 3) assess which explanatory variables (i.e. richness, rarity and threat) best explain projected Lepanthes extinction probabilities. Through these analyses, we strove to identify conservation priority areas for an import component of global plant diversity while determining whether these priority areas correspond with those identified in previous analyses. We also hoped to
determine whether conservation priority areas based on rarity can act as surrogates for overall diversity and to assess whether or not conservation priority areas based on hotspots will protect the most imminently threatened species. Lastly, we wished to ascertain which parameters are most important for identifying conservation priority areas to test the benefits and consequences of prioritizing richness, rarity or threat in planning endeavours.

METHODS

Study group

*Lepanthes* Sw. (Orchidaceae) is one of the most diverse plant genera on earth with well over 1100 described species (Luer, 1986; RBGK, 2013). This Neotropical genus occurs from Mexico to Bolivia and throughout much of the Caribbean, usually in moist to wet montane habitats at middle elevations (Luer & Theerle, 2012). While a few of these species are somewhat widespread, the vast majority have restricted distributions (Luer, 1986; Tremblay, 1997; Crain & Tremblay, 2012), making them inherently susceptible to habitat loss, stochastic disturbances and range contractions (Gaston, 1994; Gaston & Fuller, 2009). Research suggests that *Lepanthes* populations rarely persist in deforested or fragmented habitats (Sosa & Platas, 1998; Tremblay & Salguero-Faria, 2001; Vásquez et al., 2003; Soto-Arenas et al., 2007). Additionally, their high degree of ecological specialization makes *Lepanthes* spp. particularly vulnerable to extinction (Blanco & Barboza, 2005; Crain, 2012). For example, like other orchids, *Lepanthes* depend on mycorrhizal symbionts and intricate, sexually deceptive pollination mechanisms. For these reasons, *Lepanthes* has received appreciable attention from collectors, taxonomists and ecologists. Accordingly, there is an abundance of data on *Lepanthes* spp. that can be used to identify hotspots and to compare richness and rarity patterns. Moreover, the number of collection records for this group makes it well suited for use with Koopowitz’s (1992) stochastic extinction model. Consequently, the genus, *Lepanthes*, represents an ideal system for testing the applicability of combining hotspots analyses with stochastic extinction modelling to identify conservation priority areas.

Data collection

We compiled geographic data from an exhaustive list of sources to map the distribution of *Lepanthes* spp. Distribution data were primarily obtained from herbarium and botanical garden collection records, regional floras and plant checklists, and scientific publications on specific species or groups of species (see Appendix S2). Distribution data from personal observations were also included. Following protocols outlined in previous studies (Koopowitz, 1992; Koopowitz et al., 1993, 1994), records from different collectors, those with different locality names, those separated by more than 100 m in elevation and those with unique geographic coordinates were included as separate collections while equivalent records were excluded from the dataset. Each collection record constituted a single collection site, and all species collected from three or fewer sites were considered rare in our analyses.

Mapping species and rarity richness to identify hotspots

All distribution data from *Lepanthes* collection records were amassed in a table to quantify the number of species and rare species within each state, province, department, parish or region (n = 463; hereafter all subnational jurisdictions are referred to as states). This scale of analysis was chosen because it was the best resolution to maximize the number of usable collection records as not all records included geographic coordinates or more specific location descriptions. Once assembled, the data table was loaded into ARC/ESRI 10.1 [Environmental Systems Research Institute, Inc. (ESRI), Redlands, CA, USA] and joined with a background layer showing the subnational political boundaries of Latin America and the Caribbean. This process produced species richness and rare species richness distribution maps.

We analysed the data from our *Lepanthes* richness and rarity richness maps with the Hotspots Analysis (Getis-Ord Gi* Tool (ESRI, 2013) from the Spatial Statistics Toolbox to identify hotspots of species richness and rarity richness at the subnational scale. The hotspots analysis tests the null hypothesis (H0) of complete spatial randomness among the values associated with each feature by calculating *z*-scores and associated *P* values for each feature in the class; *z*-scores furthest from zero are associated with smaller *P* values and are an indication of significant spatial clustering. To run the analyses, we used subnational species richness and rarity richness values as the input feature classes. Calculations were based on Euclidian distances and an inverse distance squared conceptualization of spatial relationships. Hotspots were defined as states with *z*-scores ≥ 1.96 and associated *P* values ≤ 0.05 (ESRI, 2013).

To evaluate the degree to which richness and rarity hotspots corresponded with each other, we overlaid our richness and rarity richness hotspots layers and calculated the percentage overlap. We used Pearson’s product–moment correlation coefficients to examine the relationships between richness, rarity richness and hotspots. Results of these correlations allowed us to assess whether conservation priority areas highlighted by one of these variables could act as surrogates for the others.

Modelling extinction patterns

We used Koopowitz’s stochastic extinction model

$$E = a \sum_{n=1}^{y} b_n e^{-n}$$

and associated calculations (Koopowitz, 1992; Koopowitz et al., 1994) to forecast extinction patterns for *Lepanthes* spp. over the next 50 years due to habitat loss. To quantify the
number of predicted extinctions \((E)\) in each country, we tallied the number of species \((a)\) occurring within each nation. We then created distribution profiles (Koopowitz, 1992; Koopowitz et al., 1993) for each country to show the number of species collected from each given number of sites \((y\) is the greatest number of sites in which a species occurs) and calculated the proportions that were in each category \((b_n)\). We used the distribution profiles to calculate the number of rare species and the proportion of rare species within each country. We calculated the skewness \((g_1)\) of the distribution profiles for each country according to Sokal & Rohlf (2012). These measures were used in a subsequent analysis aimed at identifying significant predictor variables for extinction probabilities. We used data from the Food and Agriculture Organization of the United Nations spanning from 1990 to 2010 on annual changes in forest area (FAO, 2010) to calculate average annual forest conversion rates \((c)\) for each country. Specifically, we calculated the average annual rate of gain or loss in percentage of the remaining forest area in each country. After computing the predicted number of extinctions in each country, we calculated extinction probabilities \((EP)\) for each country by dividing the predicted number of extinctions by the total number of species present. As a novel approach for evaluating the relationship between hotspots and threats, the distributions of richness and rarity hotspots were compared with extinction probabilities to determine whether hotspots corresponded with high threat levels.

**Explaining extinction probabilities**

We used a nonparametric multiple regression model to assess the importance of richness, rarity and threat for explaining *Lepanthes* extinction probability patterns (Cutler et al., 2007; Grömping, 2009; Strobl et al., 2009b). Specifically, five explanatory variables were used in the model: number of species per country, number of rare species per country, proportion of rare species per country, skewness of each country’s distribution profile and annual rate of habitat loss. These variables were chosen because they are known correlates of extinction patterns and comparable types of measures are frequently used in studies aimed at identifying conservation priority areas (Brooks et al., 2006).

The regression model was run with the randomForest 4.6–7 package (Liaw & Wiener, 2002) for R version 3.0.1 Statistical Software (R Development Core Team, 2011) because of its ability to handle multiple variables, complex data distributions and small sample sizes (Cutler et al., 2007; Strobl et al., 2009a) and because each of our predictor variables were continuous (Strobl et al., 2007, 2009b). In randomForest models, two parameters: (1) \(n_{tree}\), that is, the number of regression trees to be produced in the forest and (2) \(m_{try}\), that is, the number of randomly sampled predictor variables to choose from when determining the optimal split of a given node of a tree (Liaw & Wiener, 2002), must be set to control variable selection, to diversify the trees and to stabilize results (Liaw & Wiener, 2002; Strobl et al., 2009a). For those reasons, we ran the model with \(n_{tree} = 2000\) and \(m_{try} = 2\) as suggested by Strobl et al. (2009a). In addition, we verified the stability of the forest by setting the random seed to a fixed number, 69 (Strobl et al., 2009a).

The percentage of the overall variation explained by the model was calculated in addition to the importance of the predictor variables in the model which was calculated as the percentage increase in mean-squared error \((\%\text{IncMSE})\) when they were permuted randomly. Lastly, we ranked the predictor variables in terms of \%IncMSE to highlight those that were most important for explaining extinction probability patterns for *Lepanthes* spp.

**RESULTS**

**Species richness, rarity richness and hotspots**

We amassed 4630 distribution records for 1126 species of *Lepanthes*. In terms of extent, species were distributed from central Mexico to Bolivia and on several islands in the Caribbean (Fig. 1a). In total, *Lepanthes* spp. have been documented in 163 states. Overall, Antioquia, Colombia was the richest state with a total of 123 species documented within it. Two states in Ecuador, Morona-Santiago and Zamora-Chinchipe, each contained more than 100 species while several additional states in Ecuador and Costa Rica had over 50 species recorded within their boundaries.

Of all *Lepanthes* spp., 793 were collected from three or fewer sites and considered rare according to our definition. Rare species were documented from 111 states and were distributed from southern Mexico to Bolivia and throughout the Caribbean (Fig. 1b). The greatest number of rare species, 80, was recorded from Antioquia, Colombia. Two states, Morona-Santiago and Zamora-Chinchipe, Ecuador each contained more than 45 rare species, whereas Norte de Santander, Colombia contained more than 30 rare species. Only two countries contained no rare species, Guyana and Nicaragua.

Through a spatial analysis of our *Lepanthes* species richness map, we identified 46 states (28.2% of the states in which *Lepanthes* occurs) as richness hotspots (Fig. 2a) based on the calculated Getis-Ord Gi* z-scores \((\geq 1.96)\) and their associated \(P\) values \((< 0.05)\). Consequently, we could reject the null hypothesis that these richness patterns were the result of complete spatial randomness (ESRI, 2013). The most significant hotspots, that is, those with the highest z-scores \((\geq 7.72)\), were located in northern Ecuador and in the south-western corner of Colombia. Other highly significant hotspots, albeit with slightly lower z-scores \((\geq 5.80)\), were located throughout Ecuador and in northern Colombia. Additional hotspots with significant z-scores \((\geq 1.96)\) occurred in Mexico, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru and Bolivia. No richness hotspots were identified among the Caribbean islands, from Belize to Nicaragua, or in Guyana, French Guiana, Suriname and Brazil, although *Lepanthes* spp. were distributed throughout each of these areas.
Spatial analysis of our rarity richness map led us to identify 45 states (27.6% of the states in which Lepanthes occurs) as hotspots of Lepanthes rarity (Fig. 2b) based on the calculated Getis-Ord Gi* z-scores (≥ 1.96) and the associated P values (< 0.05). As a result, we rejected the null hypothesis that these patterns were the result of complete spatial randomness (ESRI, 2013). Above all others, the most significant rarity richness hotspot was Antioquia, Colombia (z = 10.42). Highly significant rarity hotspots but with slightly lower z-scores (≥ 5.42) occurred throughout Ecuador and in western Colombia. Other significant hotspots (z ≥ 1.96) were located in Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru and Bolivia. No Lepanthes rarity richness hotspots were found north of Costa Rica, in the Caribbean, or in Guyana, French Guiana, Suriname and Brazil, although rare species occurred in each of these areas except Nicaragua and Guyana.

Overall, 42 of the 46 Lepanthes richness hotspots (91.3%) overlapped with hotspots of rarity, whereas 42 of the 45 rarity hotspots (93.3%) overlapped with Lepanthes richness hotspots (Fig 3). Only Oaxaca, Mexico, Alajuela, Costa Rica, Tolima, Colombia and Piura, Peru were identified as hotspots of species richness but did not qualify as rarity richness hotspots. Conversely, La Paz, Bolivia, Huánuco, Peru and Mérida, Venezuela were not identified as hotspots of species richness but did qualify as hotspots of rarity. Statistical analysis showed a strong positive correlation between the values of richness, rarity richness and z-scores for richness and rarity richness (Table 1; range of Pearson’s r = 0.612–0.955,

Figure 1 Distribution of (a) Lepanthes richness and (b) rare Lepanthes richness patterns at the subnational jurisdiction scale (i.e. state, province, department, parish or region). Markers in each map are scaled in size to denote the total number of species (green) or rare species (red) within the corresponding jurisdictional boundary.

Figure 2 Distribution of (a) Lepanthes richness hotspots and (b) Lepanthes rarity richness hotspots at the subnational scale (i.e. state, province, department, parish or region). The colour scales in each map designate increasing Getis-Ord Gi* z-scores (≥ 1.96) from yellow to red and decreasing associated P values (< 0.05).


Figure 3 Venn diagram showing congruence between Lepanthes richness hotspots, rarity hotspots and states in countries with the highest extinction probabilities for Lepanthes spp. Figures indicate number of states in each category and the corresponding proportion of the total number of states in which Lepanthes occurs.

Table 1 Pearson’s product–moment correlation coefficients of richness and rarity measures for each state: number of species, number of rare species, z-score based on richness patterns and z-score based on rarity patterns. All correlations are significant at \( P < 0.001 \), demonstrating significant similarities among the spatial distributions of these variables.

| Variable          | Species | Rare species | z-score (richness) |
|-------------------|---------|--------------|--------------------|
| Species           | 1       |              |                    |
| Rare species      | 0.929   | 1            |                    |
| z-score (richness)| 0.733   | 0.612        | 1                  |
| z-score (rarity)  | 0.726   | 0.685        | 0.955              |

\( P < 0.001 \), demonstrating significant similarities among the spatial distributions of these variables.

Extinction patterns

Each of the parameters calculated for use in the extinction models varied greatly among countries (Table 2). The number of species documented from each country (\( a \)) was particularly variable, ranging from 1 to 388 species (\( \mu = 57.6; SD = 94.7 \)). Ecuador and Colombia were the most species rich followed by Costa Rica, Bolivia and Guatemala. The distribution profiles for each country (e.g., Fig. 4) and the calculated values of \( b_n \) revealed that rare species, that is, those limited to three or fewer sites, were far more numerous than common ones. The number of rare species per country ranged from 1 to 264 (\( \mu = 43.6; SD = 70.7 \)) with the largest numbers of rare species occurring in Colombia, Ecuador, Costa Rica, Guatemala and Peru (Table 2). Overall, more than 70% of Lepanthes spp. were classified as rare, with the proportion of rare species in each country ranging between 11 and 100% (\( \mu = 81.6; SD = 24.1 \)). In several countries, 100% of Lepanthes species were rare (Table 2). Moreover, the distribution profile for each country was right skewed (\( g_1 = 1.17–5.00; \) Table 2) indicating a rarity trend, that is, most species occur at only a few sites. The mean annual forest conversion rate (\( c \)) for each country was between \(-2.21 \) and 3.33% per year (\( \mu = -0.31; SD = 1.09; \) Table 2).

The results from the stochastic extinction models revealed that predicted Lepanthes extinction patterns were not uniformly distributed (Table 2). On average, 7.79 (SD = 19.92) extinctions were predicted per country. The greatest numbers of extinctions were projected to occur in Ecuador, Guatemala, Colombia, Panama and Venezuela. Extinction probabilities for each country ranged from \(< 0.001 \) to 0.54 (\( \mu = 0.13; SD = 0.15 \)). The highest extinction probabilities (\( EP > 0.25 \)) were calculated for Honduras, El Salvador, Guatemala, Haiti and Ecuador.

Overall, Lepanthes richness and rarity richness hotspots only partially corresponded with high threat levels, that is, they occurred in countries with the highest extinction probabilities (Table 2; Fig. 3). In sum, 41.3% of Lepanthes richness hotspots and 42.2% of rarity richness hotspots corresponded with the highest extinction probabilities. Of the countries with the highest extinction probabilities, only Ecuador comprised states identified as hotspots of richness or rarity richness. Moreover, 19 states identified as both richness and rarity hotspots were located in Ecuador (Fig. 3), equating to 11.6% of the states where Lepanthes occurs and 38.7% of all hotspots.

Variable importance for explaining extinction patterns

The randomForest regression model explained 72.6% of the variation in Lepanthes extinction probabilities. The analysis also showed that rate of habitat loss was the most important predictor variable; %IncMSE for this variable was 46.6 and ranked first out of all variables tested. The predictor variables related to rarity were the next most important for explaining extinction probabilities. The number of rare species per country (%IncMSE = 11.3), the skewness of the distribution profile of each country (%IncMSE = 10.9) and the proportion of species in each country that were rare (%IncMSE = 8.6) followed in the predictor variable rankings in that order. The number of species in each country (%IncMSE = 7.8) ranked last among the predictor variables in terms of importance for explaining Lepanthes extinction probabilities.

DISCUSSION

Hotspots as conservation priority areas

The results of our analyses demonstrate that Lepanthes hotspots are potential conservation priority areas and emphasizing them in conservation planning could increase the efficiency of efforts to protect members of the genus. The majority of the hotspots we identified were in northeastern South America and in parts of southern Central America, and accordingly, Lepanthes hotspots largely fall within global scale conservation priority areas highlighted by previous studies (Brooks et al., 2006; Joppa et al., 2013).
Moreover, the most significant hotspots we identified largely occurred in the Tropical Andes region, which was the leading hotspot identified by Myers et al. (2000). This region has also been highlighted in recent analyses of the global patterns of vascular plant diversity (Kreft & Jetz, 2007). Consequently, our analysis suggests that conservation of global biodiversity hotspots is a suitable large-scale strategy for protecting Lepanthes spp., and alternately, that conservation of Lepanthes hotspots may be valuable for protecting a variety of other plant and animal species in Neotropical montane environments.

Unlike the patterns observed in several analyses conducted on a variety of organismal groups (Prendergast et al., 1993; Williams et al., 1996; Reyers et al., 2000; Orme et al., 2005), our results demonstrate that conservation efforts for Lepanthes spp. could be streamlined by focusing on rarity richness.

Table 2 Extinction model variables, characteristics of Lepanthes distribution profiles for each country and predicted extinction patterns. Rare species were those documented from ≤ 3 sites. Skewness ($g_1$) of each distribution profile was tested according to Sokal & Rohlf, (2012).

| Country             | # of spp. (a) | # of rare spp. | % rare | Skew ($g_1$) | % annual forest conversion rate (c) | # of extinctions ($E$) | Extinction probability ($EP$) |
|---------------------|--------------|----------------|--------|--------------|------------------------------------|------------------------|-------------------------------|
| Belize              | 5            | 4              | 80     | 4.59*        | −0.64                              | 1                      | 0.22                          |
| Bolivia             | 72           | 49             | 68     | 2.90†        | −0.46                              | 5                      | 0.08                          |
| Brazil              | 5            | 5              | 100    | 5.00*        | −0.50                              | 1                      | 0.22                          |
| Colombia            | 298          | 264            | 88     | 4.24†        | −0.16                              | 14                     | 0.04                          |
| Costa Rica          | 138          | 82             | 59     | 3.26†        | 0.08                               | 0                      | < 0.001                       |
| Cuba                | 30           | 20             | 66     | 4.06†        | 1.67                               | 0                      | < 0.001                       |
| Dominican Rep.      | 38           | 37             | 97     | 4.87†        | 0.00                               | 0                      | < 0.001                       |
| Ecuador             | 388          | 256            | 65     | 3.20†        | −1.67                              | 97                     | 0.25                          |
| El Salvador         | 14           | 14             | 100    | 4.71†        | −1.35                              | 5                      | 0.41                          |
| French Guiana       | 3            | 3              | 100    | 3.88         | −0.06                              | 0                      | 0.02                          |
| Guatemala           | 2            | 2              | 100    | 3.29         | −0.29                              | 0                      | 0.07                          |
| Guyana              | 2            | 2              | 100    | 3.29         | 0.00                               | 0                      | < 0.001                       |
| Haiti               | 19           | 19             | 100    | 5.00*        | −0.68                              | 5                      | 0.29                          |
| Honduras            | 14           | 14             | 100    | 4.48†        | −2.21                              | 7                      | 0.54                          |
| Jamaica             | 29           | 12             | 41     | 1.17†        | −0.11                              | 0                      | < 0.01                        |
| Mexico              | 63           | 29             | 46     | 1.59†        | −0.40                              | 1                      | 0.03                          |
| Nicaragua           | 11           | 7              | 63     | 2.19*        | −1.84                              | 2                      | 0.23                          |
| Panama              | 55           | 52             | 94     | 4.42†        | −0.76                              | 12                     | 0.22                          |
| Peru                | 61           | 60             | 98     | 4.93†        | −0.16                              | 4                      | 0.06                          |
| Puerto Rico         | 9            | 1              | 11     | 1.34         | 3.33                               | 0                      | < 0.001                       |
| Saint Lucia         | 1            | 1              | 100    | 5.00         | 0.3525                             | 0                      | < 0.001                       |
| Suriname            | 3            | 3              | 100    | 2.49         | 0.00                               | 0                      | < 0.001                       |
| Venezuela           | 56           | 50             | 89     | 3.92†        | −0.585                             | 8                      | 0.14                          |

*Indicates skewness is significant at 0.05. †Is significant at 0.01. Forest conversion rates are annual averages calculated from (Food & Agriculture Organization of the United Nations (FAO), 2010). Number of extinctions for each country was calculated using Koopowitz’s (1992) stochastic extinction model over 50 years. Extinction probability is calculated as the proportion of species predicted to become extinct within each country.

Figure 4 Example (Lepanthes of Ecuador) of the distribution profiles created for each country. The proportion of species that occupy given numbers of sites ($b_n$) can be calculated from the histograms for use in Koopowitz’s (1992) stochastic extinction model. Skewness of the histograms ($g_1$) can also be calculated to characterize overall rarity level within each country.
hotspots (Lawler et al., 2003) as these locations harbour the majority of all species and correspond with richness hotspots as well. These results are in accord with the similar findings of Kerr (1997) who demonstrated geographical congruence between richness and rarity patterns in some animal groups. To our knowledge, however, our analysis is one of the few to specifically focus on plants, and on orchids in particular, when comparing richness and rarity hotspots (Müller et al., 2003; Vásquez et al., 2003; Phillips et al., 2011). Consequently, additional studies are needed to determine how common congruence between richness and rarity hotspots is among various groups, particularly for plants. Such analyses will help to clarify whether it is advisable to focus on rarity richness hotspots as a method for increasing efficiency in biodiversity conservation planning (Kareiva & Marvier, 2003; Myers, 2003).

Incorporating vulnerability and threat

The distribution profiles for Lepanthes in each country indicated that rarity is the norm for this orchid group. Koopowitz et al. documented similar trends for several other orchid groups from various locations (Koopowitz, 1992; Koopowitz et al., 1993). The tendency for Lepanthes and other orchid species to be rare, as evidenced by the distribution profiles, makes them inherently more susceptible to ongoing threats such as habitat loss (Koopowitz, 1992; Gaston & Fuller, 2009). Therefore, conservation priority areas for Lepanthes spp. must incorporate patterns of vulnerability and threat to be most effective (Wilson et al., 2005).

While hotspots of richness and rarity richness were identified as potential conservation priority areas in our analysis, results from the stochastic extinction model indicated that in many cases, Lepanthes spp. were more threatened in other parts of their range. Similar patterns of incongruence between species richness, rarity richness and threat have been observed in other studies (e.g. Orme et al., 2005). Although Orme et al. (2005) analysed the distribution of bird species as opposed to plants, their results showed that hotspots of species richness and rarity richness seldom overlapped with hotspots of threatened species. Interestingly, all of the overlapping hotspots in Orme et al.’s (2005) study were located in the Andes biogeographic region, which was also where we identified overlap between Lepanthes richness hotspots, rarity hotspots and high levels of threat (i.e. high extinction probabilities). One possible explanation for this pattern is that high diversity levels are often found in heterogeneous habitats, for example montane slopes (Orme et al., 2005), which are potentially less suitable for development by humans. Overall, however, it is apparent that while richness and rarity hotspots may be efficient conservation priority areas, in most cases, there appears to be greater urgency to protect Lepanthes outside of these areas. This finding highlights the importance of considering complementarity when making conservation planning decisions (Williams et al., 1996; Reyers et al., 2000).

Strategies for Lepanthes conservation

Choosing conservation priority areas based on the combined results of our analyses should produce the most effective results for Lepanthes preservation. Because the most important explanatory variable for Lepanthes extinction probabilities was annual deforestation rate, this variable should be the initial focus for choosing conservation priority areas. In view of that, states within El Salvador, Guatemala, Honduras, Haiti and Ecuador should be prioritized due to the vulnerability of the species in these countries. Targeting hotspots within these threatened countries whenever possible, for example in Ecuador, will increase the efficiency of conservation efforts. In countries with high rates of habitat loss (FAO, 2010), reservation strategies are needed to counter rapid deforestation trends (IUCN & UNEP, 2013), particularly in the most diverse areas. The use of richness and rarity mapping methods such as those presented here can be very useful for designing reserve networks (Müller et al., 2003; Smidt et al., 2007; Tsiftsis et al., 2009). Establishing reserves is a slow process, however, and therefore ex situ strategies may also be required to protect Lepanthes spp. in the immediate future and to develop propagation and reintroduction programs (Li & Pritchard, 2009; Seaton et al., 2010). Ex situ strategies may also help buffer against the effects of global climate change, which may render currently protected habitats less suitable for Lepanthes spp. (Liu et al., 2010). These approaches are somewhat reactionary (Wilson et al., 2005; Brooks et al., 2006), however, and therefore alternate priority areas should also be considered as time and resources permit. Accordingly, a combination of in situ and ex situ strategies will likely produce the best results for conserving Lepanthes spp. (Li & Pritchard, 2009; Orejuela-Gartner, 2012).

Our results demonstrate that in addition to rates of habitat loss, measures of rarity were also important for explaining extinction probabilities. Since Lepanthes rarity richness hotspots corresponded with overall richness, they should be considered priority conservation areas as part of a more proactive approach (Wilson et al., 2005). Several rarity richness hotspots in Costa Rica, Panama, Colombia, Peru and Bolivia offer excellent opportunities to protect rare species in conjunction with overall Lepanthes diversity. As these priority areas are less threatened than others, for example those in Ecuador, but still harbour inherently vulnerable species, conservation strategies should focus on reserve establishment, range size expansion and population management in these locations (Gaston, 1994; Tremblay & Hutchings, 2002).

CONCLUSIONS

Combining hotspots analyses with stochastic extinction models is an effective means to identify specific conservation priority areas that incorporate measures of richness, rarity and threat. The hotspots highlighted in this analysis of Lepanthes spp. largely corresponded with priority areas identified in global analyses of other species groups, thus adding to the body of
evidence suggesting that global biodiversity hotspots (e.g. Myers et al., 2000) are important conservation priorities for a number of species groups. Still, not all hotspots highlighted in global analyses, for example, the Caribbean (Myers et al., 2000; Brooks et al., 2006), were identified as hotspots in this analysis, and therefore, smaller scale analyses for individual groups are justified for identification of the most appropriate conservation priority areas.

Because Lepanthes richness and rarity hotspots largely overlapped, it is apparent that in some cases, conservation of rare species could inadvertently help to protect overall species diversity. Additional analyses are needed, however, to determine how frequently this pattern holds true because similar studies on other groups have produced conflicting results. Nevertheless, this analysis demonstrates that conservation efforts can be streamlined in some instances by focusing on rarity richness hotspots.

Through the use of a stochastic extinction model (Koopowitz, 1992; Koopowitz et al., 1994), we were able to forecast Lepanthes extinction patterns and incorporate vulnerability and threat into conservation prioritization. In doing so, we corroborated prior evidence showing that richness and rarity do not necessarily correspond with threat (Orme et al., 2005). This finding reinforces arguments that vulnerability and threat need to be included in conservation planning efforts (Wilson et al., 2005; Brooks et al., 2006).

To conclude, this study is intended to aid in Lepanthes conservation by stimulating focused analyses on species within the conservation priority areas identified here. In addition, this study should provide a useful guide for conducting similar analyses of additional orchid genera as well as other plant and animal groups. Accordingly, as hotspots analyses and extinction models are amassed, conservation priority areas will become more refined, and biodiversity preservation efforts will become more efficient and effective.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Underlying assumptions of the Koopowitz stochastic extinction model.

**Appendix S2** Sources of distribution data used in this analysis.

**BIOSKETCHES**

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