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Biogeographical analyses to facilitate targeted conservation of orchid diversity hotspots in Costa Rica

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Abstract

Aim: We conduct a biogeographical assessment of orchids in a global biodiversity hotspot to explore their distribution and occurrences of local hotspots while identifying geographic attributes underpinning diversity patterns. We evaluate habitat characteristics associated with orchid diversity hotspots and make comparisons to other centres of orchid diversity to test for global trends. The ultimate goal was to identify an overall set of parameters that effectively characterize critical habitats to target in local and global orchid conservation efforts.

Location: Costa Rica; Mesoamerica.

Taxon: Orchidaceae.

Methods: Data from an extensive set of herbarium records were used to map orchid distributions and to identify diversity hotspots. Hotspot data were combined with geographic attribute data, including environmental and geopolitical variables, and a random forest regression model was utilized to assess the importance of each variable for explaining the distribution of orchid hotspots. A likelihood model was created based on variable importance to identify locations where suitable habitats and unidentified orchid hotspots might occur.

Results: Orchids were widely distributed and hotspots occurred primarily in mountainous regions, but occasionally at lower elevations. Precipitation and vegetation cover were the most important predictive variables associated with orchid hotspots. Variable values underpinning Costa Rican orchid hotspots were similar to those reported at other sites worldwide. Models also identified suitable habitats for sustaining orchid diversity that occurred outside of known hotspots and protected areas.

Main conclusions: Several orchid diversity hotspots and potentially suitable habitats occur outside of known distributions and/or protected areas. Recognition of these sites and their associated geographic attributes provides clear targets for optimizing orchid conservation efforts in Costa Rica, although certain caveats warrant consideration. Habitats linked with orchid hotspots in Costa Rica were similar to those documented elsewhere, suggesting the existence of a common biogeographical trend regarding critical habitats for orchid conservation in disparate tropical regions.

KEYWORDS
biodiversity hotspot, Costa Rica, critical habitat, distribution mapping, orchids (Orchidaceae), plant conservation, random forest model, spatial ecology, species richness, weighted sum model

1 | INTRODUCTION

Biodiversity conservation is a pressing concern requiring detailed knowledge of biogeographical patterns and the ecological relationships underpinning them (Wallington, Hobbs, & Moore, 2005; Whittaker et al., 2007). Identifying and prioritizing biodiversity hotspots along with their associated ecological correlates is a prominent method for optimizing conservation efforts (Cañadas et al., 2014; Joppa, Roberts, Myers, & Pimm, 2011; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Empirical studies advise that incorporating diversity hotspots into conservation planning strategies is particularly valuable for protecting biodiversity worldwide (Brooks et al., 2006; Cowling, Pressey, Rouget, & Lombard, 2003; Posa, Diesmos, Sodhi, & Brooks, 2008; Sodhi, Butler, Laurance, & Gibson, 2011; Torres-Santana, Santiago-Valentín, Sánchez, Peguero, & Clubbe, 2010). Accordingly, hotspot research, including development of methods for their identification and conservation, is an important approach for biodiversity preservation.

The Mesoamerican global biodiversity hotspot has been highlighted for many reasons, including its exceptionally large number of endemic plants (Myers et al., 2000). Research shows, however, that species richness is unevenly distributed within global hotspots, and local priorities need to be established (Cañadas et al., 2014; Harris, Jenkins, & Pimm, 2005; Médail & Quézel, 1997, 1999; Murray-Smith et al., 2009). Studies also indicate there is little correspondence between hotspots of various taxonomic groups (Prendergast, Quinn, Lawton, Eversham, & Gibbons, 1993; Reid, 1998). Consequently, detailed analyses of specific taxonomic groups at finer geographic scales are necessary to identify conservation priorities within global diversity hotspots.

Within the Mesoamerica biodiversity hotspot, Costa Rica is extremely diverse and noteworthy for its rich flora (Hammel-Lierheimer, Grayum, Herrera-Mora, Zamora-Villalobos, & Troyo-Jiménez, 2004; Janzen, 1983). Taxonomically, the orchid family (Orchidaceae Juss.) is well represented there, comprising a significant portion of the overall diversity in the country and in Mesoamerica (Dressler, 1993; Hammel-Lierheimer, Grayum, Herrera-Mora, Zamora-Villalobos, & Troyo-Jiménez, 2003). Analysis of the spatial distribution of orchids and their biogeographical relationships is critical for understanding orchid ecology, evaluating protected areas and identifying conservation targets in Costa Rica and elsewhere (Liu et al., 2010).

The overall objective of this study was to investigate the spatial distribution and geographic affinities of orchids in Costa Rica to identify underlying factors driving diversity patterns. We aimed to answer the following questions: 1) How are orchids distributed in Costa Rica and where do diversity hotspots occur? 2) What geographic variables most strongly influence the distribution of orchid hotspots? 3) Where are the most suitable habitats for potentially undocumented orchid diversity hotspots in Costa Rica? We hypothesize that orchid diversity patterns are linked to specific geographic conditions and that suitable habitats and potentially undocumented hotspots exist outside of currently protected areas. Results from this analysis will improve our understanding of fundamental biogeographical patterns in Costa Rica, Mesoamerica and other biodiversity hotspots. They will also support calls to identify potential *Important Orchid Areas* (IOAs), that is sites with exceptionally rich orchid floras and/or important habitats for their conservation (Seaton, Kendon, Pritchard, Puspitaningtyas, & Marks, 2013), much like *Important Plant Areas* (IPAs; Anderson, 2002; Foster et al., 2012). Ultimately, our results will advance conservation efforts by pinpointing specific targets for protecting an important component of global plant biodiversity.

2 | METHODS

2.1 | Study site

Costa Rica has an exceptional orchid flora that is well studied (Hammel-Lierheimer et al., 2003). The country is renowned for its commitment to orchid biology and conservation, and extensive resources for documenting orchid diversity and distributions are available (Blanco, Pupulin, & Warner, 2005; Bogarín, Pupulin, Arrocha, & Warner, 2013; Pupulin, 2007; Rivero, 1998). Consequently, the Costa Rican orchid flora represents a unique opportunity to evaluate biogeographical affinities of the family within a global diversity hotspot.

2.2 | Mapping orchid occurrences and richness hotspots

To map orchid distribution patterns in Costa Rica, we used collection records from the National Museum of Costa Rica (CR), the Lankester Botanical Garden (JBL) and the National Biodiversity Institute (INB) herbaria, which house the largest collections in the country (Thiers, 2015). We amassed distribution data from 12,316 records representing 1,320 orchid species. Geographic coordinates from each record were imported into ArcGIS 10.1 (Environmental Systems Research Institute, 2011) to create a point layer showing the distribution of orchids throughout the country. A network of 1-km^2 grid cells spanning the country was created, and the number of species in each cell was quantified. The resulting layer was used as the input feature class in the hotspot analysis (Getis-Ord Gi*) tool to identify hotspots of orchid diversity, defined as grid cells with z-scores ≥ 1.96 and associated $p \le 0.05$ (Environmental Systems Research Institute, 2014; see Appendix S1 in Supporting Information for detailed methodology).

2.3 | Characterizing geographic attributes of orchid hotspots

To quantify geographic attributes associated with orchid hotspots in Costa Rica, we used GIS data layers for environmental and geopolitical variables characterizing the country (Ortiz-Malavasi, 2009; Table 1). Environmentally, we focused on abiotic and biotic variables that have known potential to influence orchid communities and their distribution. We considered biotemperature and precipitation because they have been shown to be limiting factors for several orchid species physiologically and ecologically (Crain & Tremblay, 2017; Liu et al., 2010; Vollering, Schuiteman, Vogel, Vugt, & Raes, 2015). Orchids can also be bound to particular forest levels (e.g. lowland or montane), terrain characteristics (i.e. slopes) and elevation ranges, each of which was included in our models, due to potential effects on microclimates, disturbance regimes and breeding systems (Jacquemyn, Micheneau, Roberts, & Pailler, 2005; Pupulin, 1998; Vollering et al., 2015; Whitman, Medler, Randriamanindry, & Rabakonandrianina, 2011). The Holdridge life zone system incorporates measures of biotemperature, precipitation and evapotranspiration to predict climax vegetation patterns (Holdridge, 1947), and thus, we included this attribute as an additional predictor variable. Soil attributes were accounted for in our models because they can influence the distribution of terrestrial orchids and their mycorrhizal associates (e.g. McCormick et al., 2012; Phillips, Brown, Dixon, & Hopper, 2010). Soils may also influence the distribution of potential host trees, vegetation types and habitats that are suited to epiphytic orchids (Gentry & Dodson, 1987). The final environmental variables we considered were vegetation cover and land use/land cover, as orchids can be limited to specific vegetation types, such as primary forests (Pupulin, 1998), and may be differently adapted or susceptible to various land uses, for example, agriculture or logging (Sosa & Platas, 1998).

Geopolitically, we focused on two government jurisdiction levels (province and county, i.e. cantón) to determine whether regional and local jurisdictions differ in terms of orchid diversity patterns that rise from differences in conservation priorities at the regional versus local scales (Porras, 2010; Pressey, Mills, Weeks, & Day, 2013). We also focused on attributes of the protected areas in the country and considered potential differences in nine regional conservation areas, the different types of protected areas (e.g. national parks or wildlife areas) and the individual protected areas, which can differ in terms of regulations and management (Evans, 1999; Sistema Nacional de Áreas de Conservación (SINAC), 2012, 2013, 2014). The size of each protected area was the final geopolitical variable considered in our models, as it is a known correlate of orchid species richness estimates (Schödelbauerová, Roberts, & Kindlmann, 2009).

TABLE 1 Geographic attributes (environmental and geopolitical variables) from the Atlas Costa Rica (Ortiz-Malavasi, 2009) tested for associations with orchid diversity hotspots and used to identify suitable habitats

Geographic attributes	
Environmental variables	**Geopolitical variables**
Forest level	Province[a]
Holdridge life zone[a]	County (Cantón)
Elevation range (m a.s.l.)[a]	Conservation area[a]
Terrain characteristics[a]	Protected area type[a]
Vegetation cover[a]	Protected area
Land use/Land cover[a]	Protected area size (ha)[a]
Biotemperature range(C°)	
Mean annual precipitation (mm)[a]	
Soil type (order[a], suborder[a] and great group)	

[a]Indicates variables used in the final random forest regression model for explaining the distribution of hotspots.

2.4 | Modelling geographic suitability for orchid hotspots

To identify locations in Costa Rica with the greatest potential to support undocumented hotspots of orchid diversity based on habitat suitability, we quantified the proportion of each variable value's distribution that was identified as an orchid diversity hotspot. Variable values with larger proportions of their distribution corresponding with hotspots were considered more characteristic of potentially suitable habitat (Appendix S2.2).

We evaluated the overall importance of each geographic attribute for explaining the distribution of orchid hotspots by running a series of nonparametric random forest regression models (Breiman, 2001; Cutler et al., 2007; Liaw & Wiener, 2002; Strobl, Hothorn, & Zeileis, 2009; Appendix S1). Random forest models have been increasingly utilized in ecological applications and can offer several improvements over more traditional models (Cutler et al., 2007). We chose the random forest modelling approach specifically for its ability to handle large datasets efficiently and for its capacity to include numerous input variables (Rodriguez-Galiano, Ghimire, Rogan, Chica-Olmo, & Rigol-Sanchez, 2012). It is also well suited to deal with categorical variables, variable interactions and outliers (Breiman, 2001; Cutler et al., 2007; Rodriguez-Galiano et al., 2012). Moreover, random forest modelling approaches are very useful for assessing the importance of specific predictor variables (Cutler et al., 2007; Grömping, 2009; Rodriguez-Galiano et al., 2012; Strobl, Malley, & Tutz, 2009). The importance of the explanatory variables (i.e. geographic attributes) in our analysis was evaluated by calculating the per cent increase in mean squared error (%IncMSE) when individual variables were permuted randomly (Grömping, 2009).

We combined the habitat suitability measures and the importance estimates of each geographic attribute in a weighted sum model (e.g. Ananda & Herath, 2009; Phua & Minowa, 2005; Store & Jokimäki, 2003) to quantify the geographic suitability (*Suitability*$_i$) of each grid cell in our map (Appendix S1). We used the suitability values from the weighted sum model to generate a new map documenting locations most likely to support orchid diversity hotspots based on their geographic attributes.

3 | RESULTS

3.1 | Orchid occurrences in Costa Rica

Our distribution map revealed that orchids have been documented in 2,680 1-km^2 grid cells (5.1% of the country; Figure 1). Cells with the greatest number of species (≥100 spp; n = 2) occurred in the Cordillera de Tilarán. Cells with 50 to 99 species (n = 9) were also documented in the Cordillera de Tilarán, as well as in the Cordillera de Guanacaste, in the Cordillera Central and in the northern parts of

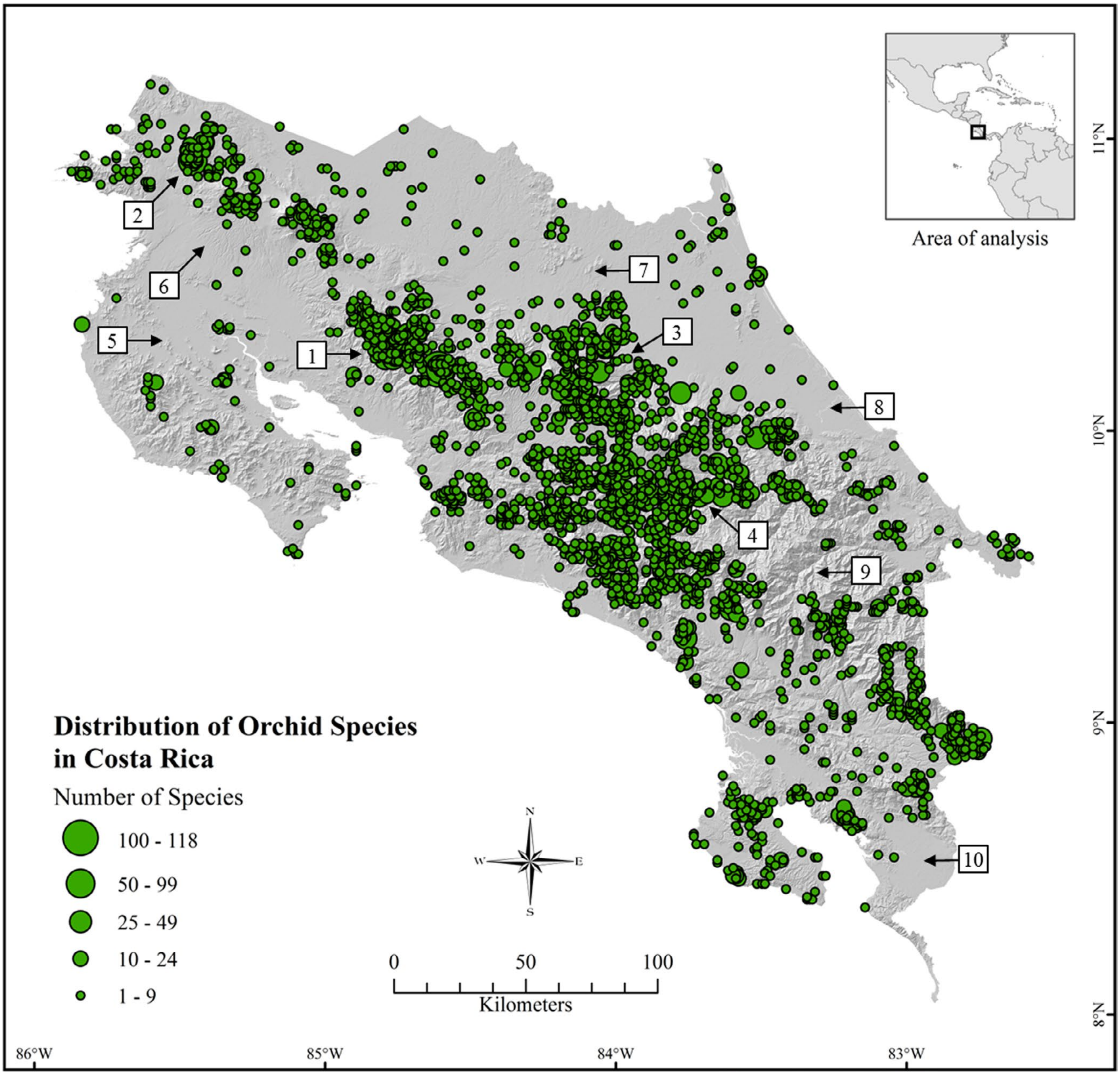

FIGURE 1 Distribution of orchid diversity in Costa Rica based on number of species present in 1-km^2 grid cells. Larger markers indicate a greater abundance of orchid species in a given cell. Numbered arrows indicate areas where cells with the greatest number of orchid species are located: 1) Cordillera de Tilarán, 2) Cordillera de Guanacaste, 3) Cordillera Central, 4) northern Cordillera de Talamanca, and areas where orchids were documented less frequently: 5) Nicoya Peninsula, 6) Guanacaste Lowlands, 7) San Carlos Plains, 8) Caribbean Lowlands, 9) central Cordillera de Talamanca and 10) Golfito and Punta Burica region

the Cordillera de Talamanca. Orchid species occurred less frequently on the Nicoya Peninsula and in the lowlands of Guanacaste in northwest Costa Rica, the San Carlos Plains in the far north, the Caribbean Lowlands, the central portion of the Cordillera de Talamanca and the extreme southern tip of the country between Golfito and Punta Burica, although inaccessibility and limitations to collecting may play roles in the latter two regions. Overall, the distribution map suggests that Costa Rican orchids occur primarily in centrally located mountainous regions of the country, but with notable exceptions.

3.2 | Hotspots of orchid diversity in Costa Rica

The hotspot analysis identified 5,684 grid cells, representing 10.8% of the country, as significant hotspots of orchid diversity ($p \le .05$; Figure 2). Large clusters of hotspot cells occurred in mountainous regions (generally between 1,000 and 2000 m a.s.l.) in the Cordillera de Guanacaste, the Cordillera de Tilarán, the Cordillera Central and the north-western and south-eastern portions of the Cordillera de Talamanca. Hotspots at lower elevation sites (generally below 1,000 m a.s.l.) occurred near Puerto Viejo de Sarapiquí on the Atlantic slope, on the Osa Peninsula, along the Golfo Dulce region in southern Costa Rica and in the Pacific coastal foothills, for example. Notably, hotspots were not identified on the Nicoya Peninsula although orchids have been documented throughout much of the region.

Clusters of the most significant hotspot cells (Getis-Ord G^* z-scores ≥ 21.429101) occurred in three distinct areas (Figure 2). The largest of them (n = 93) occurred in the Cordillera de Tilarán in and around the Monteverde Biological Reserve. A second cluster (n = 5) occurred in the Cordillera Central near Parque Nacional Braulio Carrillo. A final cluster (n = 53) occurred in the Cordillera de Talamanca near Parque Nacional Tapantí. Collectively, these three areas comprising 151 km^2 represented the most significant orchid diversity hotspots in the country.

3.3 | Geographic attributes of orchid hotspots in Costa Rica

Linking geographic attributes to known orchid diversity hotspots highlighted the most frequently associated environmental and geopolitical variable values (Appendix S2.1). Among environmental variables, the largest percentage of hotspots occurred at 1400–1499 m a.s.l. elevation (7.1%). The largest percentages of hotspots also corresponded with biotemperatures between 18 and 24°C (50.1%) and mean annual precipitation levels between 3,500 and 4,000 mm (20.5%). For land cover types, forested areas accounted for the greatest percentage of hotspots (39.5%), and among forest levels, pre-montane forests had the largest proportion (50.1%). The pluvial pre-montane forest Holdridge life zone corresponded with the most hotspots (24.1%). Among specific land use/land cover types, the most hotspots corresponded with areas categorized as natural primary forest (58.7%). For terrain types, the largest proportion of hotspots (46.5%) occurred in locations categorized as very hilly with 30%–60% slopes. Among soil types, the largest percentages of hotspots corresponded with the Ultisols soil order (52.4%), the Humults suborder (49.0%) and the Tropohumults great group (49.0%).

Geopolitically (Appendix S2.1), the largest percentage of orchid diversity hotspots (23.9%) occurred in the San José Province, but among counties (cantones) the greatest proportion of hotspots (8.3%) was in San Ramón, Alajuela. The largest percentage of hotspots was distributed within the Central Volcanic Conservation Area (30.1%). The greatest proportion of hotspots corresponding with protected areas occurred in national parks (25.2%), while the Los Santos Forest Reserve encompassed the largest individual proportion among all protected areas (7.0%). Larger protected areas, for example, the Los Santos Forest Reserve and Braulio Carrillo National Park, tended to support greater percentages of hotspots (7.0% and 5.4%, respectively). Alternatively, 41.4% of hotspots, including 50 of the most significant cells, were not associated with protected areas.

3.4 | Geographic suitability for orchid hotspots

Our direct focus on geographic attributes allowed us to identify habitat characteristics with the greatest suitability likelihoods for orchid diversity hotspots (i.e. attributes with the largest proportions of their distribution occupied by identified hotspots; Appendix S2.2). Among environmental variables, hotspots overlapped with the largest overall proportion of cells occurring between 1,700 and 1799 m a.s.l. (49.2%). Hotspots occupied the greatest proportions of cells with average biotemperatures between 12 and 18°C (42.5%) and mean precipitation levels between 6,500 and 7,500 mm (88.1%). Cells in the lower montane forest level (42.5%) and the humid lower montane forest Holdridge life zone (81.2%) were occupied by hotspots in the greatest portions of their ranges. Regarding land use/land cover, natural primary forest was occupied by hotspots in the largest percentage of its distribution (23.8%), whereas for vegetation cover types, coffee agriculture was most likely to be occupied by hotspots (22.7%). Concerning terrain, cells categorized as very hilly with 30%–60% slopes were most likely to be occupied by hotspots (18.6%). For soils, the Inceptisols order (14.6%), the Andepts suborder (28.0%) and the Hydrandepts great group (51.3%) were most frequently occupied by hotspots.

Among geopolitical variable values most likely to be occupied by hotspots, San José ranked first among provinces (29.4%) while El Guarco, Cartago, ranked first among counties (cantones) with 100% overlap (Appendix S2.2). For conservation areas and protected area types, the Arenal Tilarán Conservation Area (32.2%) and protected zones (39.6%) were most likely to be occupied by hotspots. Hotspots occupied 100% of eight individual protected areas: Caraigres and Río Navarro-Río Sombrero Protected Zones; La Cangreja National Park; Cerro Las Vueltas Biological Reserve; Curi Cancha, Donald Peter Hayes and Jaguarundi Wildlife Refuges; and Laguna del Paraguas Palustrine Wetlands.

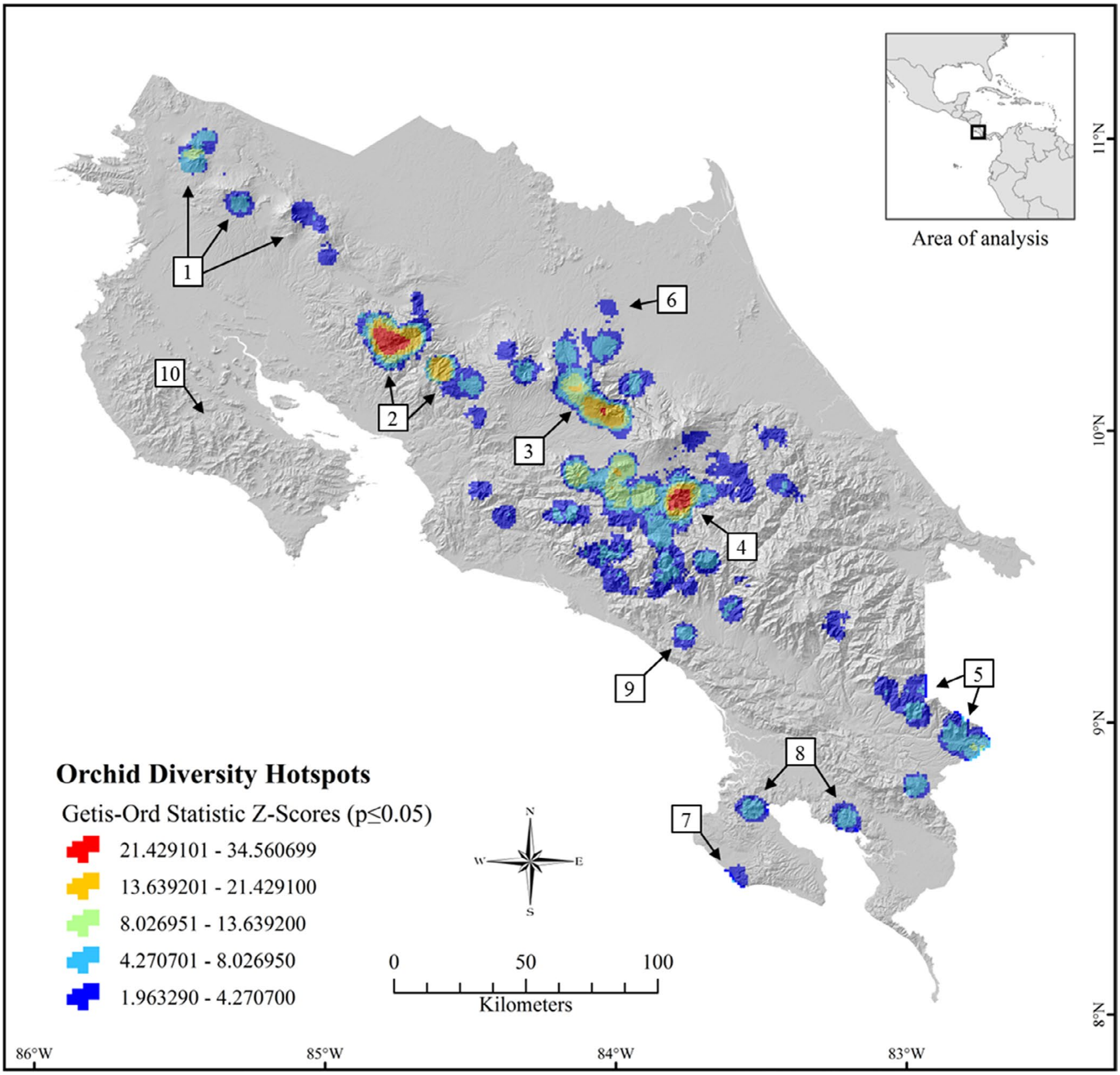

FIGURE 2 Distribution of orchid diversity hotspots in Costa Rica based on spatial clustering of 1-km^2 grid cells occupied by large numbers of orchid species. Hotspots were identified as grid cells with Getis-Ord Gi* z-scores ≥ 1.96 and associated p ≤ .05. Numbered arrows indicate large clusters of hotspots occurring in 1) Cordillera de Guanacaste, 2) Cordillera de Tilarán, 3) Cordillera Central, 4) northern Cordillera de Talamanca, 5) southern Cordillera de Talamanca, 6) Puerto Viejo de Sarapiquí region, 7) Osa Peninsula, 8) Golfo Dulce region and 9) Pacific coastal foothills. The largest clusters of the most significant hotspot cells (Getis-Ord G* z-scores ≥ 21.429101) occurred in 2) Cordillera de Tilarán, 3) Cordillera Central and 4) northern Cordillera de Talamanca. Hotspots were notably absent on 10) the Nicoya Peninsula

Results from the random forest model based on specific geographic attribute values allowed us to pinpoint the most important variables for explaining the distribution of orchid diversity hotspots. Among tested models, the model including 12 variables (eight environmental and four geopolitical) explained the largest percentage of the overall variation (85.15%; Table 1). Environmental and geopolitical variables both ranked highly in terms of explanatory power based on per cent increase in mean squared error (%IncMSE) values (Figure 3). Mean annual precipitation was the most important explanatory variable (%IncMSE = 163.72) followed by vegetation cover (%IncMSE = 114.59). The next most important variables were province (%IncMSE = 110.77) and conservation area (%IncMSE = 109.24). The remaining variables in the model had considerably less explanatory power (%IncMSE = 80.73–38.89).

The habitat suitability map created from the weighted sum model results highlights appropriate areas for orchid diversity

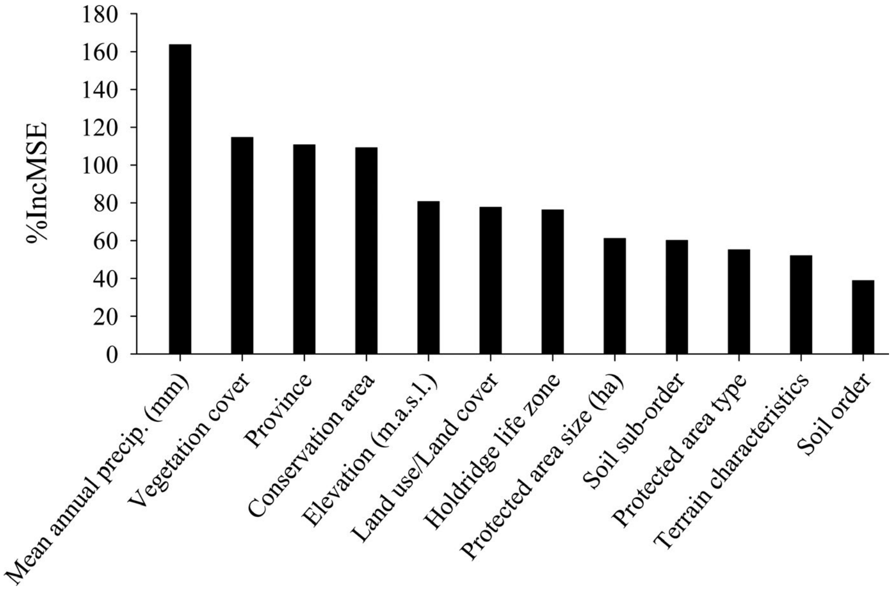

FIGURE 3 Explanatory power (%IncMSE) of geographic attributes (environmental and geopolitical variables) in the random forest regression model explaining the distribution of orchid diversity hotspots in Costa Rica. Overall, the model explained 85.15% of the variation. The %IncMSE values were used to calculate variable weights (w_j) in a weighted sum model

hotspots based on geographic attributes (Figure 4). Suitability estimates for individual grid cells ranged from 0.01 to 0.34 ($\bar{x}$ = 0.10, *SD* = 0.05). Cells with the largest suitability measures ($Suitability_i$ ≥ 0.197853, *n* = 4,255) were considered most likely to support hotspots.

Geographically suitable areas were widespread, but the majority of the most suitable areas were in mountainous regions (Figure 4). The largest cluster of highly suitable cells (*n* = 3,606) occurred in central Costa Rica and extended from the Cordillera Central to the north-west portion of the Cordillera de Talamanca. Two smaller clusters (*n* = 21 and 20) were located in the mountains near Turrubares and Puriscal. A fourth cluster (*n* = 273) was located in the Cordillera de Tilarán. Three additional clusters (*n* = 14, 61 and 41) occurred in the Cordillera de Guanacaste. A final cluster of the most geographically suitable cells (*n* = 219) was situated in the Cordillera de Talamanca near the Panama border.

Of all hotspot cells, 40.7% overlapped with the most geographically suitable habitats for orchid diversity identified by our model. This total increased to 85.9% when considering the top two suitability categories ($Suitability_i$ ≥ 0.146191; *n* = 13,005). Concerning only the most significant hotspots, 58.2% coincided with cells having the highest suitability estimates whereas 97.3% overlapped with cells in the top two categories. Only 14.1% of all hotspots and 2.6% of the most significant hotspots occurred outside areas with the top two habitat suitability measures. Furthermore, only 1.8% of all hotspot cells and none of the most significant hotspots corresponded with the two lowest habitat suitability categories.

Among cells predicted to be most geographically suitable, 54.3% were identified as hotspots in our analysis. For cells in the second highest suitability category (0.146191 ≤ $Suitability_i$ <0.197853; *n* = 8,750), 29.3% were identified as hotspots. Consequently, large proportions of cells predicted to be highly suitable for orchid diversity hotspots were not identified as such by our model based on collection records.

4 | DISCUSSION

4.1 | Orchid distribution patterns

As a vital component of plant diversity in the Mesoamerican global biodiversity hotspot, it is unsurprising that Orchidaceae, one of the largest and most widespread plant families (Chase et al., 2015; Dressler, 2005), was well represented throughout Costa Rica (Figure 1). Like other hotspots, Costa Rica is geographically heterogeneous, having unique habitats along two coasts and among four main mountain ranges (Burger, 1980; Janzen, 1983; Kirby, 2011). Such features are conducive to high plant diversity levels and abundant pollinator pools that may facilitate dispersal and diversification (Acharya, Vetaas, & Birks, 2011; Crain & White, 2013; Gentry & Dodson, 1987; Kirby, 2011; Roubik & Hanson, 2004; Trapnell & Hamrick, 2005; Zhang, Yan, et al., 2015). Thus, there are extensive opportunities for geographic specialization and speciation among various ecological niches for orchids that may explain the breadth of their distribution in Costa Rica (Burger, 1980; Gentry & Dodson, 1987; Kirby, 2011).

Still, some parts of Costa Rica are notably devoid of orchids (Figure 1). This finding is consistent with other orchid distribution studies in similarly diverse regions. For example, orchids are abundant and widespread in other Mesoamerican countries such as Panama and Mexico (Dressler, 2005; Hágsater & Arenas, 1998), but more profuse in geographically heterogeneous regions therein (Bogarín, Serracín, Samüdiü, Rincón, & Püpülin, 2014; Castillo-Pérez, Martínez-Soto, Maldonado-Miranda, Alonso-Castro, & Carranza-Álvarez, 2018; Kirby, 2011; Soto-Arenas, Gómez, & Hágsater, 2015). Distributional voids within these countries primarily stem from comparable geographic and ecological attributes. Most sites lacking orchids are lowland areas characterized by hot and dry climates (Bogarín et al., 2014; Kirby, 2011; Soto-Arenas et al., 2015). Consequently, specific geographic and ecological attributes undoubtedly play a key role in determining

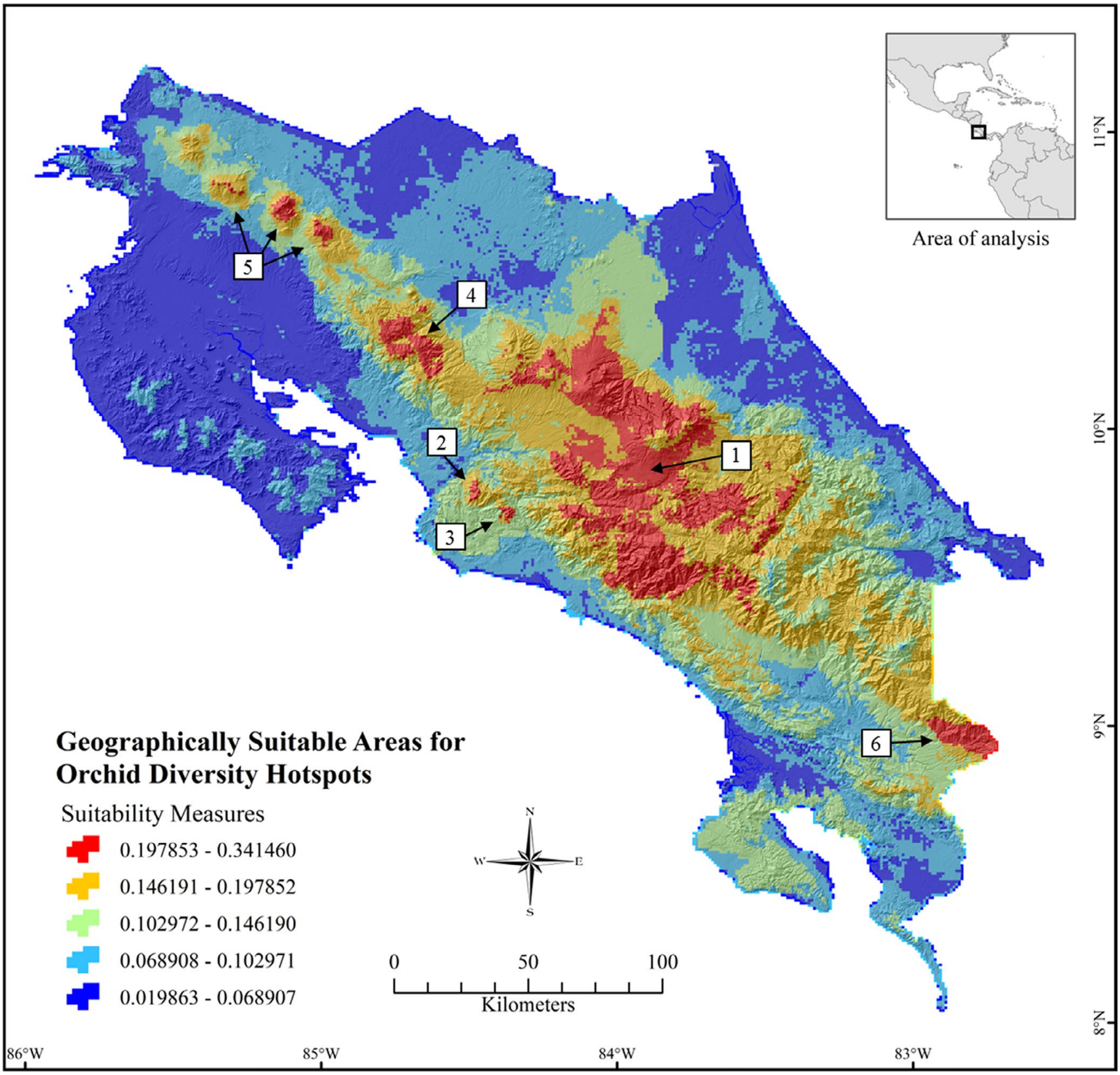

FIGURE 4 Distribution of geographically suitable areas for orchid diversity hotspots in Costa Rica based on geographic attributes, including environmental and geopolitical variables (Table 1). Suitability measures of all 1-km^2 grid cells ($Suitability_i$) were derived from a weighted sum model integrating the performance measures of individual variable values in each cell (a_{ij}) and the corresponding variable weights (w_j). Numbered arrows indicate areas with large clusters of the most suitable habitats: 1) central Costa Rica including Cordillera Central and northern Cordillera de Talamanca, 2) Turrubares area, 3) Puriscal area, 4) Cordillera de Tilarán, 5) Cordillera de Guanacaste and 6) southern Cordillera de Talamanca

the local distribution of orchids in Costa Rica and elsewhere, although differences in survey intensity may contribute to the pattern.

4.2 | Orchid diversity hotspots and *Important Orchid Areas*

While orchids occurred throughout most of the country, distinct hotspots were identifiable. This finding can facilitate the identification of potential *IOAs* (Seaton et al., 2013) following general criteria established for *IPAs* (Anderson, 2002) by highlighting sites with exceptionally rich orchid floras and/or important habitats for their conservation. From a conservation perspective, the distribution of orchid hotspots is encouraging since the majority corresponded with protected areas. Hotspots not corresponding with protected areas represent important conservation targets, however (Seaton, 2007), particularly the 50 cells that are among the richest hotspots. A large proportion of unprotected hotspots are adjacent to existing protected areas, and small expansions of these preserves could help protect them. The remaining hotspots could be prioritized as new protected areas are established. Because orchid hotspots frequently correspond with diversity centres for other species groups, protection of these locations would provide ancillary benefits for biodiversity conservation beyond orchids (Anderson, Cherrington, Flores, et al., 2008; Anderson, Cherrington, Tremblay-Boyer, Flores, & Sempris, 2008; Kohlmann et al., 2010; Kohlmann, Solis, Elle, Soto, & Russo, 2007; Seaton, 2007).

4.3 | Underlying geography of orchid hotspots

Analysing geographic attributes associated with orchid diversity hotspots enabled us to identify the most important environmental and geopolitical features supporting orchid diversity in Costa Rica. These geographic attributes were comparable to those highlighted in studies of other locations and species groups.

Mountainous middle-elevation forests correlated strongly with orchid diversity, and their significance has been emphasized in studies worldwide (Acharya et al., 2011; Bogarín et al., 2014; Hágsater & Arenas, 1998; Jacquemyn, Honnay, & Pailler, 2007; Jacquemyn et al., 2005; Krömer, Kessler, Robbert Gradstein, & Acebey, 2005; Linder, Kurzweil, & Johnson, 2005; Liu et al., 2015; Müller, Nowicki, Barthlott, & Ibisch, 2003; Orejuela-Gartner, 2012; Tsiftsis, Tsiripidis, & Trigas, 2011; Vollering et al., 2015; Zhang, Chen, Huang, Bi, & Yang, 2015; Zhang, Yan, et al., 2015). These settings provide a variety of environmental conditions, and habitat heterogeneity is commonly cited as an important driver of diversity (Crain & White, 2013; Zhang, Yan, et al., 2015). Studies on orchid distribution and diversification in Central and South America theorize that recent geologic events, including rapid growth of mountain ranges, volcanic activity and glaciation at high elevations, are primary drivers of orchid evolution and speciation (Dodson, 2003; Kirby, 2011). Our results showing peak diversity levels in mountainous areas supported this assertion. Studies on other tropical plant and animal communities have produced similar findings (Gentry & Dodson, 1987; Kluge, Kessler, & Dunn, 2006; Kohlmann et al., 2007, 2010; Krömer et al., 2005; McCain, 2004). There were exceptions, however, as some hotspots occurred at coastal lowland sites (Figure 2), suggesting various local geographic attributes can support orchid diversity and must be accounted for in conservation planning.

Precipitation levels and temperature ranges associated with orchid hotspots in Costa Rica were comparable to those characterizing hotspots documented elsewhere (Acharya et al., 2011; Zhang, Chen, et al., 2015). Large varieties of epiphytic plant groups achieve maximum diversity levels under similar conditions (Gentry & Dodson, 1987). It is suggested that optimal water–energy dynamics obtained under cool moist conditions promote high biodiversity levels and our results fit this claim (O'Brien, 2006). Furthermore, the cool moist conditions associated with hotspots in Costa Rica are similar to those promoting inflorescence and flower development in some orchids (Blanchard & Runkle, 2006), thus providing another possible explanation for their abundance at those sites.

Soil characteristics were not as strongly linked with the distribution of orchid hotspots, which may be related to the primarily epiphytic habit of most orchids, but interesting patterns still emerged. Orchid hotspots were generally found in moist, weathered, mineral soils that are relatively infertile. While some evidence indicates that epiphyte diversity is generally higher on fertile soils (Gentry & Dodson, 1987), our results did not support this since hotspots were uncommon or absent in the most fertile soil types in the country, for example, Mollisols, Alfisols and Entisols. Soil characteristics might affect the distribution of potential host trees and mycorrhizal fungi, however (Gentry & Dodson, 1987; Phillips et al., 2010), and these factors might explain the connection between orchid hotspots and soil types in Costa Rica. The fact that soil order and suborder were significant variables in our regression model suggests that soil characteristics are important attributes related to the distribution of orchids and should be considered when evaluating prospective habitats.

Concerning land use/land cover types as well as vegetation cover in Costa Rica, our results support documented trends from other locations and organismal groups. Orchid hotspots most frequently coincided with natural primary forests, whose value to orchid richness and overall biodiversity has been repeatedly recognized (Barthlott, Schmit-Neuerburg, Nieder, & Engwald, 2001; Gibson et al., 2011; Hundera et al., 2013). Nevertheless, a number of hotspots corresponded with less pristine habitats, including coffee plantations. This is not entirely surprising, however, as cool, humid, middle-elevation sites that are prime habitats for many orchids are also ideal for coffee production (Moguel & Toledo, 1999; Perfecto, Rice, Greenberg, & Van der Voort, 1996). Some studies even show that populations of orchids, epiphytes and other species can be well maintained in coffee plantations (Moguel & Toledo, 1999; Solis-Montero, Flores-Palacios, & Cruz-Angón, 2005; Sosa & Platas, 1998; Williams-Linera, Sosa, & Platas, 1995). Still, other studies show that diversity of orchids and other species in coffee plantations is variable and largely dependent on specific management strategies; intensively, farmed areas are generally less diverse (Hundera et al., 2013; Philpott et al., 2008). Consequently, research on coffee plantations and orchid diversity in Costa Rica is warranted to determine whether richness levels are a result of specific management strategies maintaining crucial properties of natural forests.

Geopolitically, our results support findings of other biodiversity studies in Costa Rica (see Janzen, 1983; Nadkarni & Wheelwright, 2000). In most cases, the highest diversity levels were associated with existing protected areas, particularly within the Central Volcanic and Arenal-Tilarán Conservation Areas, which encompass large portions of diverse habitats in the Cordillera de Tilarán and the Cordillera Central. Several national parks exist in these regions, and of the various protected area types in Costa Rica, national parks support the largest proportion of orchid hotspots. Although this pattern was somewhat expected since the national park system in Costa Rica includes many of the oldest and largest protected areas with strict conservation regulations (Brüggemann, 1997), it highlights the importance of these parks. Large proportions of protected zones were also occupied by orchid hotspots, and they could be targeted for increased attention and regulation concerning orchid conservation.

While correspondence between hotspots and protected areas highlights the significance of conservation efforts in Costa Rica, it may also be indicative of species and habitat losses outside these safe havens. The majority of orchid hotspots occurred in provinces with the highest population densities, which may point to high threat levels for hotspots outside protected areas (Rosero-Bixby & Palloni, 1998; Sánchez-Azofeifa, Harriss, & Skole, 2001). Consequently, unprotected hotspots near encroaching development and high population centres need attention from conservation planners. Expanding existing reserves while establishing smaller ones in strategic areas would be viable options for protecting additional orchid diversity centres.

4.4 | Geographic suitability and orchid conservation applications

Our geographic models suggest environmental and geopolitical variables are valuable predictors of orchid diversity in Costa Rica. Habitat suitability estimates accurately coincided with the majority of known hotspots. Thus, our modelling approaches offer a useful framework for evaluating suitable habitats for orchid hotspots. These methods are broadly applicable, although specific variable values will be unique in other regions (Bernardos, García-Barriuso, Ángeles Sánchez-Anta, & Amich, 2007; Linder et al., 2005; Phillips et al., 2010; Vogt-Schilb, Munoz, Richard, & Schatz, 2015), and similar studies in other orchid diversity centres are encouraged to help determine the generality of trends observed in Costa Rica. Thus far, however, the patterns observed in Costa Rica are in close accord with findings from other areas that have been evaluated (Acharya et al., 2011; Liu et al., 2015; Müller et al., 2003; Vollering et al., 2015; Zhang, Chen, et al., 2015), and it appears that models incorporating similar geographic attributes will be fitting for predicting distributions of orchid diversity hotspots in other areas.

Identifying connections between geographic attributes and orchid hotspots will ultimately benefit conservation efforts in many ways. Geographic suitability models will help optimize efforts to identify and protect undocumented hotspots. Geographically suitable locations not yet identified as hotspots could be targeted for floristic surveys and analysis. If seemingly ideal habitats do not support hotspots, it may point to other factors limiting orchid diversity, such as inadequate pollinator populations or mycorrhizal associates, that must be addressed (Reiter et al., 2016). In either case, habitat suitability mapping should help streamline orchid conservation efforts.

Understanding links between orchid hotspots and geographic characteristics should also prove useful for implementing translocation or reintroduction projects. Geographically suitable areas may offer important alternatives for mitigating habitat losses or disturbances in other parts of orchid species' ranges (Crain & Tremblay, 2014; Reiter et al., 2016; Seaton et al., 2013). Early identification of suitable areas may also be useful for assisted migration efforts for combating range shifts due to global climate change (Anderson, Cherrington, Tremblay-Boyer, et al., 2008; Crain & Tremblay, 2017; Liu et al., 2010; Reiter et al., 2016; Seaton, Hu, Perner, & Pritchard, 2010). With the aid of habitat suitability estimates, these conservation measures are more likely to succeed because appropriately chosen translocation sites will reflect orchids' natural habitats and may be more likely to support pollinators or mycorrhizal symbionts (Reiter et al., 2016).

4.5 | Caveats and considerations for future research

While our study presents a useful framework for analysing biogeographical underpinnings of orchid diversity and the results should provide valuable information for advancing the development of systematic targeted conservation plans in Costa Rica, there are several caveats to consider when interpreting geographic analyses of biodiversity over larger regional scales. It is important to note that while diversity hotspots may represent efficient targets for conservation efforts, not all orchid species will be distributed in these locales (Kareiva & Marvier, 2003). Orchids occurring outside of hotspots, particularly rare species, must not be neglected as they are likely to have unique attributes and/or ecological significance in their own settings. Additionally, our analysis makes use of orchid diversity estimates within each individual grid cell to identify hotspots for conservation targets, but does not explore beta diversity across the collective network of hotspots, which will be an important consideration for conservation decision-makers and a worthwhile extension of this study (Socolar, Gilroy, Kunin, & Edwards, 2016). Furthermore, our analysis does not include an assessment of phylogenetic diversity or conservation status (e.g. rarity or threat) of orchids, which will be important considerations for providing optimal benefits for preserving various components of overall orchid diversity within the hotspot network (Crain & Tremblay, 2014; Swenson, 2011). A final caveat of biodiversity research using GIS to look at species and habitat distributions over larger spatial scales is that species' distributions and actual on-site habitat conditions do not necessarily equate with model predictions, particularly at very small scales. Accordingly, systematic assessments of species' statuses and actual habitat conditions within individual hotspots should be conducted through targeted field surveys and/or detailed, remotely sensed data to confirm the suitability and significance of individual hotspots identified in our analyses.

5 | CONCLUSIONS

Understanding the biogeography of orchids in Costa Rica is a crucial step towards the conservation of this important component of biodiversity. The world's orchid flora is incredibly unique and widespread, and hotspots warrant significant attention from scientists, conservation agencies and local stakeholders. By analysing geographic attributes associated with orchid hotspots, including environmental and geopolitical variables, critical factors related to their distribution can be identified and explored to understand ecological relationships, identify suitable habitats and document conservation targets. Our findings highlight the importance of analysing the complex geographic patterns and ecological underpinnings of orchid diversity hotspots and will help researchers and conservation practitioners take necessary steps towards preserving orchids in the most important centres of biological diversity.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the National Museum of Costa Rica (CR) at http://ecobiosis.museocostarica.go.cr/. Data for non-type herbarium specimens from the Lankester Botanical Garden (JBL) are available at http://epidendra.org/Herbarium/index.htm, while data for type specimens are available at http://epidendra.org/Herbarium/types.htm. JBL has restricted locality data to maintain confidentiality about the exact location of threatened orchids' populations; bona fide researchers and institutions can request complete data from JBL. Data from the National Biodiversity Institute (INBio) can be accessed at http://specify7.museocostarica.go.cr:8080/specify-solr/.

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REFERENCES

Acharya, K. P., Vetaas, O. R., & Birks, H. J. B. (2011). Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography*, *38*, 1821–1833. https://doi.org/10.1111/j.1365-2699.2011.02511.x

Ananda, J., & Herath, G. (2009). A critical review of multi-criteria decision making methods with special reference to forest management and planning. *Ecological Economics*, *68*, 2535–2548. https://doi.org/10.1016/j.ecolecon.2009.05.010

Anderson, E. R., Cherrington, E. A., Flores, A. I., Perez, J. B., Carillo, R., & Sempris, E. (2008). *Potential impacts of climate change on biodiversity in Central America, Mexico, and the Dominican Republic*. Panama City, Panama: Water center for the humid tropics of latin America and the Caribbean/United States agency for International Development.

Anderson, E. R., Cherrington, E. A., Tremblay-Boyer, L., Flores, A. I., & Sempris, E. (2008). Identifying critical areas for conservation: Biodiversity and climate change in central America, Mexico, and the Dominican Republic. *Biodiversity*, *9*, 89–99. https://doi.org/10.1080/14888386.2008.9712912

Anderson, S. (2002). *Identifying important plant areas*. London, UK: Plantlife International.

Barthlott, W., Schmit-Neuerburg, V., Nieder, J., & Engwald, S. (2001). Diversity and abundance of vascular epiphytes: A comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. *Plant Ecology*, *152*, 145–156.

Bernardos, S., García-Barriuso, M., Ángeles Sánchez-Anta, M., & Amich, F. (2007). Composition, geographical affinities and endemism of the Iberian Peninsula orchid flora. *Nordic Journal of Botany*, *25*, 227–237. https://doi.org/10.1111/j.0107-055X.2007.00123.x

Blanchard, M. G., & Runkle, E. S. (2006). Temperature during the day, but not during the night, controls flowering of *Phalaenopsis* orchids. *Journal of Experimental Botany*, *57*, 4043–4049. https://doi.org/10.1093/jxb/erl176

Blanco, M. A., Pupulin, F., & Warner, J. (2005). Conservation of Costa Rican orchids: The role of Lankester Botanical Garden. *Selbyana*, *26*, 356–357. https://doi.org/10.1093/jxb/erl176

Bogarín, D., Pupulin, F., Arrocha, C., & Warner, J. (2013). Orchids without borders: Studying the hotspot of Costa Rica and Panama. *Lankesteriana*, *13*, 13–26. https://doi.org/10.15517/lank.v0i0.11529

Bogarín, D., Serracín, Z., Samüdiü, Z., Rincón, R., & Püpülin, F. (2014). An updated checklist of the Orchidaceae of Panama. *Lankesteriana*, *14*, 135–364.

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32.

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., … Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, *313*, 58–61. https://doi.org/10.1126/science.1127609

Brüggemann, J. (1997). National parks and protected area management in Costa Rica and Germany: A comparative analysis. In K. Ghimire & M. P. Pimbert (Eds.), *Social change and conservation: Environmental politics and impacts of national parks and protected areas* (pp. 71–96). London, UK: Earthscan Publications Ltd.

Burger, W. C. (1980). Why are there so many kinds of flowering plants in Costa Rica? *Brenesia*, *17*, 371–388.

Cañadas, E. M., Fenu, G., Peñas, J., Lorite, J., Mattana, E., & Bacchetta, G. (2014). Hotspots within hotspots: Endemic plant richness, environmental drivers, and implications for conservation. *Biological Conservation*, *170*, 282–291. https://doi.org/10.1016/j.biocon.2013.12.007

Castillo-Pérez, L. J., Martínez-Soto, D., Maldonado-Miranda, J. J., Alonso-Castro, A. J., & Carranza-Álvarez, C. (2018). The endemic orchids of Mexico: A review. *Biologia*, *74*, 1–13. https://doi.org/10.2478/s11756-018-0147-x

Chase, M. W., Cameron, K. M., Freudenstein, J. V., Pridgeon, A. M., Salazar, G., Berg, C., & Schuiteman, A. (2015). An updated classification of Orchidaceae. *Botanical Journal of the Linnean Society*, *177*, 151–174. https://doi.org/10.1111/boj.12234

Cowling, R. M., Pressey, R. L., Rouget, M., & Lombard, A. T. (2003). A conservation plan for a global biodiversity hotspot—The Cape Floristic Region, South Africa. *Biological Conservation*, *112*, 191–216. https://doi.org/10.1016/S0006-3207(02)00425-1

Crain, B. J., & Tremblay, R. L. (2014). Do richness and rarity hotspots really matter for orchid conservation in light of anticipated habitat loss? *Diversity and Distributions*, *20*, 652–662. https://doi.org/10.1111/ddi.12179

Crain, B. J., & Tremblay, R. L. (2017). Hot and bothered: Changes in microclimate alter chlorophyll fluorescence measures and increase stress levels in tropical epiphytic orchids. *International Journal of Plant Sciences*, *178*, 503–511. https://doi.org/10.1086/692767

Crain, B. J., & White, J. W. (2013). A checklist and floristic summary of the vascular plants of Napa County, California. *Phytotaxa*, *95*, 1–60. https://doi.org/10.11646/phytotaxa.95.1.1

Cutler, D. R., Edwards, T. C. Jr, Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*, 2783–2792. https://doi.org/10.1890/07-0539.1

Dodson, C. H. (2003). Why are there so many orchid species? *Lankesteriana*, *7*, 99–103.

Dressler, R. L. (1993). *Field guide to the orchids of Costa Rica and Panama* (1st ed.). Ithaca, NY: Cornell University Press.

Dressler, R. L. (2005). How many orchid species? *Selbyana*, *26*, 155–158.

Environmental Systems Research Institute Inc. (ESRI). (2011). *ArcGIS, 10.1*.

Environmental Systems Research Institute Inc. (ESRI). (2014) *ArcGIS Help 10.2, 10.2.1, and 10.2.2: Hot Spot Analysis (Getis-Ord Gi*) (Spatial Statistics)*. Retrieved from http://resources.arcgis.com/en/help/main/10.2/index.html#//005p00000010000000

Evans, S. (1999). *The Green Republic: A conservation history of Costa Rica*, (1st ed.). Austin, TX: University of Texas Press.

Foster, M. N., Brooks, T. M., Cuttelod, A., De Silva, N., Fishpool, L. D. C., Radford, E. A., & Woodley, S. (2012). The identification of sites of biodiversity conservation significance: Progress with the application of a global standard. *Journal of Threatened Taxa*, *4*, 2733–2744.

Gentry, A. H., & Dodson, C. H. (1987). Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, *74*, 205–233. https://doi.org/10.2307/2399395

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., … Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*, 378–381. https://doi.org/10.1038/nature10425

Grömping, U. (2009). Variable importance assessment in regression: Linear regression versus random forest. *The American Statistician*, *63*, 308–319. https://doi.org/10.1198/tast.2009.08199

Hágsater, E., & Arenas, M. A. S. (1998). Orchid conservation in Mexico. *Selbyana*, *19*, 15–19.

Hammel-Lierheimer, B. E., Grayum, M. H., Herrera-Mora, C., Zamora-Villalobos, N. A., & Troyo-Jiménez, S. (2003). *Manual de Plantas de Costa Rica. Volumen III. Monocotiledóneas (Orchidaceae-Zingiberaceae)*. St. Louis, MO: Missouri Botanical Garden.

Hammel-Lierheimer, B. E., Grayum, M. H., Herrera-Mora, C., Zamora-Villalobos, N. A., & Troyo-Jiménez, S. (2004). *Manual de Plantas de Costa Rica. Volumen I. Introduction*. St. Louis, MO: Missouri Botanical Garden Press.

Harris, G. M., Jenkins, C. N., & Pimm, S. L. (2005). Refining biodiversity conservation priorities. *Conservation Biology*, *19*, 1957–1968. https://doi.org/10.1111/j.1523-1739.2005.00307.x

Holdridge, L. (1947). Determination of world plant formations from simple climatic data. *Science*, *105*, 367–368. https://doi.org/10.1126/science.105.2727.367

Hundera, K., Aerts, R., De Beenhouwer, M., Van Overtveld, K., Helsen, K., Muys, B., & Honnay, O. (2013). Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen afromontane forests. *Biological Conservation*, *159*, 285–291. https://doi.org/10.1016/j.biocon.2012.10.029

Jacquemyn, H., Honnay, O., & Pailler, T. (2007). Range size variation, nestedness and species turnover of orchid species along an altitudinal gradient on Réunion Island: Implications for conservation. *Biological Conservation*, *136*, 388–397. https://doi.org/10.1016/j.biocon.2006.12.008

Jacquemyn, H., Micheneau, C., Roberts, D. L., & Pailler, T. (2005). Elevational gradients of species diversity, breeding system and floral traits of orchid species on Reunion Island. *Journal of Biogeography*, *32*, 1751–1761. https://doi.org/10.1111/j.1365-2699.2005.01307.x

Janzen, D. H. (1983). *Costa Rican natural history*, (1st ed.). Chicago, IL: University of Chicago Press.

Joppa, L. N., Roberts, D. L., Myers, N., & Pimm, S. L. (2011). Biodiversity hotspots house most undiscovered plant species. *Proceedings of the National Academy of Sciences*, *108*, 13171–13176. https://doi.org/10.1073/pnas.1109389108

Kareiva, P., & Marvier, M. (2003). Conserving biodiversity coldspots. *American Scientist*, *91*, 344–351. https://doi.org/10.1511/2003.4.344

Kirby, S. (2011). Active mountain building and the distribution of "core" Maxillariinae species in tropical Mexico and Central America. *Lankesteriana*, *11*, 275–291. https://doi.org/10.15517/lank.v11i3.18283

Kluge, J., Kessler, M., & Dunn, R. R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, *15*, 358–371. https://doi.org/10.1111/j.1466-822X.2006.00223.x

Kohlmann, B., Roderus, D., Elle, O., Solís, Á., Soto, X., & Russo, R. (2010). Biodiversity conservation in Costa Rica: A correspondence analysis between identified biodiversity hotspots (Araceae, Arecaceae, Bromeliaceae, and Scarabaeinae) and conservation priority life zones. *Revista Mexicana de Biodiversidad*, *81*, 511–559.

Kohlmann, B., Solis, A., Elle, O., Soto, X., & Russo, R. (2007). Biodiversity, conservation, and hotspot atlas of Costa Rica: A dung beetle perspective (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa*, *1457*, 1–34.

Krömer, T., Kessler, M., Robbert Gradstein, S., & Acebey, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography*, *32*, 1799–1809. https://doi.org/10.1111/j.1365-2699.2005.01318.x

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, *2*, 18–22.

Linder, H. P., Kurzweil, H., & Johnson, S. D. (2005). The southern African orchid flora: Composition, sources and endemism. *Journal of Biogeography*, *32*, 29–47. https://doi.org/10.1111/j.1365-2699.2004.01202.x

Liu, H., Feng, C.-L., Luo, Y.-B., Chen, B.-S., Wang, Z.-S., & Gu, H.-Y. (2010). Potential challenges of climate change to orchid conservation in a wild orchid hotspot in southwestern China. *The Botanical Review*, *76*, 174–192. https://doi.org/10.1007/s12229-010-9044-x

Liu, Q., Chen, J., Corlett, R. T., Fan, X., Yu, D., Yang, H., & Gao, J. (2015). Orchid conservation in the biodiversity hotspot of southwestern China. *Conservation Biology*, *29*, 1563–1572. https://doi.org/10.1111/cobi.12584

McCain, C. M. (2004). The mid-domain effect applied to elevational gradients: Species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*, 19–31. https://doi.org/10.1046/j.0305-0270.2003.00992.x

McCormick, M. K., Taylor, D. L., Juhaszova, K., Burnett, R. K. Jr, Whigham, D. F., & O'Neill, J. P. (2012). Limitations on orchid recruitment: Not a simple picture. *Molecular Ecology*, *21*, 1511–1523. https://doi.org/10.1111/j.1365-294X.2012.05468.x

Médail, F., & Quézel, P. (1997). Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. *Annals of the Missouri Botanical Garden*, *84*, 112–127. https://doi.org/10.2307/2399957

Médail, F., & Quézel, P. (1999). Biodiversity hotspots in the Mediterranean Basin: Setting global conservation priorities. *Conservation Biology*, *13*, 1510–1513. https://doi.org/10.1046/j.1523-1739.1999.98467.x

Moguel, P., & Toledo, V. M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology*, *13*, 11–21. https://doi.org/10.1046/j.1523-1739.1999.97153.x

Müller, R., Nowicki, C., Barthlott, W., & Ibisch, P. L. (2003). Biodiversity and endemism mapping as a tool for regional conservation planning–case study of the Pleurothallidinae (Orchidaceae) of the Andean rain forests in Bolivia. *Biodiversity & Conservation*, *12*, 2005–2024.

Murray-Smith, C., Brummitt, N. A., Oliveira-Filho, A. T., Bachman, S., Moat, J., Lughadha, E. M., & Lucas, E. J. (2009). Plant diversity hotspots in the Atlantic coastal forests of Brazil. *Conservation Biology*, *23*, 151–163. https://doi.org/10.1111/j.1523-1739.2008.01075.x

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*, 853–858. https://doi.org/10.1038/35002501

Nadkarni, N. M., & Wheelwright, N. T. (2000). *Monteverde: Ecology and conservation of a tropical cloud forest*. Oxford, UK: Oxford University Press.

O'Brien, E. M. (2006). Biological relativity to water–energy dynamics. *Journal of Biogeography*, *33*, 1868–1888. https://doi.org/10.1111/j.1365-2699.2006.01534.x

Orejuela-Gartner, J. E. (2012). Orchids of the cloud forests of southwestern Colombia and opportunities for their conservation. *European Journal of Environmental Sciences*, *2*, 19–32. https://doi.org/10.14712/23361964.2015.84

Ortiz-Malavasi, E. (2009). *Atlas digital de Costa Rica 2008*. Cartago, Costa Rica: Instituto Tecnológico de Costa Rica.

Perfecto, I., Rice, R. A., Greenberg, R., & Van der Voort, M. E. (1996). Shade coffee: A disappearing refuge for biodiversity. *BioScience*, *46*, 598–608. https://doi.org/10.2307/1312989

Phillips, R. D., Brown, A. P., Dixon, K. W., & Hopper, S. D. (2010). Orchid biogeography and factors associated with rarity in a biodiversity hotspot, the Southwest Australian Floristic Region. *Journal of Biogeography*, *38*, 487–501. https://doi.org/10.1111/j.1365-2699.2010.02413.x

Philpott, S. M., Arendt, W. J., Armbrecht, I., Bichier, P., Diestch, T. V., Gordon, C., … Zolotoff, J. M. (2008). Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. *Conservation Biology*, *22*, 1093–1105. https://doi.org/10.1111/j.1523-1739.2008.01029.x

Phua, M.-H., & Minowa, M. (2005). A GIS-based multi-criteria decision making approach to forest conservation planning at a landscape scale: A case study in the Kinabalu Area, Sabah, Malaysia. *Landscape and Urban Planning*, *71*, 207–222. https://doi.org/10.1016/j.landurbplan.2004.03.004

Porras, I. (2010). *Fair and green? Social impacts of payments for environmental services in Costa Rica*. London, UK: International Institute for Environment and Development.

Posa, M. R. C., Diesmos, A. C., Sodhi, N. S., & Brooks, T. M. (2008). Hope for threatened tropical biodiversity: Lessons from the Philippines. *BioScience*, *58*, 231–240. https://doi.org/10.1641/B580309

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, *365*, 335–337. https://doi.org/10.1038/365335a0

Pressey, R. L., Mills, M., Weeks, R., & Day, J. C. (2013). The plan of the day: Managing the dynamic transition from regional conservation designs to local conservation actions. *Biological Conservation*, *166*, 155–169. https://doi.org/10.1016/j.biocon.2013.06.025

Pupulin, F. (1998). Orchid florula of Parque Nacional Manuel Antonio, Quepos, Costa Rica. *Revista de Biología Tropical*, *46*, 961–1031.

Pupulin, F. (2007). Epidendra, the botanical databases of Jardín Botánico Lankester at the University of Costa Rica. *Lankesteriana*, *7*, 178–180.

Reid, W. V. (1998). Biodiversity hotspots. *Trends in Ecology & Evolution*, *13*, 275–280. https://doi.org/10.1016/S0169-5347(98)01363-9

Reiter, N., Whitfield, J., Pollard, G., Bedggood, W., Argall, M., Dixon, K., … Swarts, N. (2016). Orchid re-introductions: An evaluation of success and ecological considerations using key comparative studies from Australia. *Plant Ecology*, *217*, 81–95. https://doi.org/10.1007/s11258-015-0561-x

Rivero, R. E. (1998). Targeting orchids and other epiphytes in a conservation education program in Costa Rica. *Selbyana*, *19*, 20–26.

Rodriguez-Galiano, V. F., Ghimire, B., Rogan, J., Chica-Olmo, M., & Rigol-Sanchez, J. P. (2012). An assessment of the effectiveness of a random forest classifier for land-cover classification. *ISPRS Journal of Photogrammetry and Remote Sensing*, *67*, 93–104. https://doi.org/10.1016/j.isprsjprs.2011.11.002

Rosero-Bixby, L., & Palloni, A. (1998). Population and deforestation in Costa Rica. *Population and Environment*, *20*, 149–185.

Roubik, D. W., & Hanson, P. E. (2004). *Orchid Bees of Tropical America: Biology and Field Guide*. Heredia, Costa Rica: Instituto Nacional de Biodiversidad (INBio).

Sánchez-Azofeifa, G. A., Harriss, R. C., & Skole, D. L. (2001). Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. *Biotropica*, *33*, 378–384.

Schödelbauerová, I., Roberts, D. L., & Kindlmann, P. (2009). Size of protected areas is the main determinant of species diversity in orchids. *Biological Conservation*, *142*, 2329–2334. https://doi.org/10.1016/j.biocon.2009.05.015

Seaton, P. (2007). Orchid conservation: Where do we go from here? *Lankesteriana*, *7*, 13–16. https://doi.org/10.15517/lank.v7i1-2.18385

Seaton, P. T., Hu, H., Perner, H., & Pritchard, H. W. (2010). Ex situ conservation of orchids in a warming world. *The Botanical Review*, *76*, 193–203. https://doi.org/10.1007/s12229-010-9048-6

Seaton, P., Kendon, J. P., Pritchard, H. W., Puspitaningtyas, D. M., & Marks, T. R. (2013). Orchid conservation: The next ten years. *Lankesteriana*, *13*, 93–101. https://doi.org/10.15517/lank.v0i0.11545

Sistema Nacional de Áreas de Conservación (SINAC). (2012). *Plan General de Manejo Zona Protectora Cerros de La Carpintera: Gestión Participativa para la Conservación del Agua y la Biodiversidad*. San José, Costa Rica: SINAC.

Sistema Nacional de Áreas de Conservación (SINAC). (2013). *Plan General de Manejo Reserva Natural Absoluta Nicolas Wessberg*. Costa Rica, San José: SINAC.

Sistema Nacional de Áreas de Conservación (SINAC) (2014). *Plan General de Manejo Parque Nacional Tapantí-Macizo de la Muerte*. Costa Rica: San José: SINAC.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, *31*, 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Sodhi, N. S., Butler, R., Laurance, W. F., & Gibson, L. (2011). Conservation successes at micro-, meso-and macroscales. *Trends in Ecology & Evolution*, *26*, 585–594. https://doi.org/10.1016/j.tree.2011.07.002

Solis-Montero, L., Flores-Palacios, A., & Cruz-Angón, A. (2005). Shade-coffee plantations as refuges for tropical wild orchids in central Veracruz, Mexico. *Conservation Biology*, *19*, 908–916. https://doi.org/10.1111/j.1523-1739.2005.00482.x

Sosa, V., & Platas, T. (1998). Extinction and persistence of rare orchids in Veracruz, Mexico. *Conservation Biology*, *12*, 451–455. https://doi.org/10.1046/j.1523-1739.1998.96306.x

Soto-Arenas, M., Gómez, R. S., & Hágsater, E. (2015). Risk of extinction and patterns of diversity loss in Mexican orchids. *Lankesteriana*, *7*, 114–121. https://doi.org/10.15517/lank.v7i1-2.18449

Store, R., & Jokimäki, J. (2003). A GIS-based multi-scale approach to habitat suitability modeling. *Ecological Modelling*, *169*, 1–15. https://doi.org/10.1016/S0304-3800(03)00203-5

Strobl, C., Hothorn, T., & Zeileis, A. (2009). Party on! A new, conditional variable-importance measure for random forests available in the party package. *The R Journal*, *1*, 14–17. https://doi.org/10.32614/RJ-2009-013

Strobl, C., Malley, J., & Tutz, G. (2009). An introduction to recursive partitioning: Rationale, application and characteristics of classification and regression trees, bagging and random forests. *Psychological Methods*, *14*, 323–348. https://doi.org/10.1037/a0016973

Swenson, N. G. (2011). The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany*, *98*, 472–480. https://doi.org/10.3732/ajb.1000289

Thiers, B. (2015). *Index herbariorum: A global directory of public herbaria and associated staff*. Retrieved form http://sweetgum.nybg.org/ih/

Torres-Santana, C. W., Santiago-Valentín, E., Sánchez, Á., Peguero, B., & Clubbe, C. (2010). Conservation status of plants in the Caribbean island biodiversity hotspot. In Anonymous (Ed.), *Proceedings of the Fourth Global Botanic Gardens Congress*, *June 2010* (Vol. 4, pp 1–15). Dublin. http://www.bgci.org/files/Dublin2010/papers/Torres-Santana-Christian.pdf

Trapnell, D. W., & Hamrick, J. L. (2005). Mating patterns and gene flow in the neotropical epiphytic orchid, *Laelia rubescens*. *Molecular Ecology*, *14*, 75–84. 294X.2004.02383.x

Tsiftsis, S., Tsiripidis, I., & Trigas, P. (2011). Identifying important areas for orchid conservation in Crete. *European Journal of Environmental Sciences*, *1*, 28–37. https://doi.org/10.14712/23361964.2015.44

Vogt-Schilb, H., Munoz, F., Richard, F., & Schatz, B. (2015). Recent declines and range changes of orchids in western Europe (France, Belgium and Luxembourg). *Biological Conservation*, *190*, 133–141. https://doi.org/10.1016/j.biocon.2015.05.002

Vollering, J., Schuiteman, A., Vogel, E., Vugt, R., & Raes, N. (2015). Phytogeography of New Guinean orchids: Patterns of species richness and turnover. *Journal of Biogeography*, *43*, 204–214. https://doi.org/10.1111/jbi.12612

Wallington, T. J., Hobbs, R. J., & Moore, S. A. (2005). Implications of current ecological thinking for biodiversity conservation: A review of the salient issues. *Ecology and Society*, *10*, 1–15. https://doi.org/10.5751/ES-01256-100115

Whitman, M., Medler, M., Randriamanindry, J. J., & Rabakonandrianina, E. (2011). Conservation of Madagascar's granite outcrop orchids: The influence of fire and moisture. *Lankesteriana*, *11*, 55–67. https://doi.org/10.15517/lank.v11i1.18315

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M., & Willis, K. J. (2007). Conservation biogeography: Assessment and prospect. *Diversity and Distributions*, *11*, 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Williams-Linera, G., Sosa, V., & Platas, T. (1995). The fate of epiphytic orchids after fragmentation of a Mexican cloud forest. *Selbyana*, *16*, 36–40.

Zhang, S.-B., Chen, W.-Y., Huang, J.-L., Bi, Y.-F., & Yang, X.-F. (2015). Orchid species richness along elevational and environmental gradients in Yunnan, China. *PLoS ONE*, *10*, 1–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Zhang, Z., Yan, Y., Tian, Y., Li, J., He, J.-S., & Tang, Z. (2015). Distribution and conservation of orchid species richness in China. *Biological Conservation*, *181*, 64–72. https://doi.org/10.1016/j.biocon.2014.10.026

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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