Richness and endemism centers of mega genus *Astragalus* (Fabaceae) in Iran

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Abstract

**Richness and endemism centers of mega genus *Astragalus* (Fabaceae) in Iran.** — Iran is the main center of speciation and endemicism of *Astragalus* (Fabaceae), the largest flowering plant genus in the Old World. The areas of endemism and major endemic hotspots of this genus are not well known, and detailed spatial evaluation is required using several GIS-based approaches. In this paper, spatial endemism patterns of *Astragalus* in Iran were studied using species richness, parsimony analysis of endemicity (PAE) and geographical interpolation of endemism (GIE) approaches. We collected 4180 distribution records for 589 *Astragalus* endemics from all available resources. On the basis of the richness map, three endemic hotspots were found for *Astragalus* in Iran. Also, seven and four areas of endemism (AoEs), were identified using GIE and PAE analysis, respectively. Atropatanean is the richest province for Iranian *Astragalus* endemics. The majority of the areas of endemism are located in the mountainous habitats of Iran such as Alborz, Zagros, Khorassan-Kopet Dagh as well as the central and southern highlands of Iran. Our findings showed that the mountains play an important role in *Astragalus* endemicity, but plains, salt marshes and rangelands also harbor numerous endemic species, so they should also be given priority for conservation. The results of the three approaches are largely consistent with each other. However, it seems that the PAE was able to operate much more successfully than the other two approaches and cover most the areas of endemism of *Astragalus* in Iran. Finally, we suggest that in biogeographic studies in Iran, grid cell-based techniques and circular neighborhood approaches should be used together to determine areas with conservation priority.

Key words: biogeography; endemism; Fabaceae; PAE; species richness.

Resumen

**Centros de riqueza y endemismo del megagénero *Astragalus* (Fabaceae) en Irán.** — Irán es el principal centro de especiación y endemismo de *Astragalus* (Fabaceae), el mayor género de angiospermas en el viraje mundo. Las áreas de endemismo y los hotspots de endemismo del género no son bien conocidos y es necesaria una evaluación detallada utilizando aproximaciones SIG. En este artículo, se estudian los patrones de distribución espacial de los endemismos del género *Astragalus* en Irán utilizando la riqueza de especies, el análisis parsimonioso de endemicidad (PAE por sus siglas en inglés) y la interpolación geográfica de endemismo (GIE por sus siglas en inglés). Utilizando todas las fuentes disponibles, se han reunido 4180 citas para 589 endemismos de *Astragalus*. Han sido identificados tres hotspots así como siete y cuatro áreas de endemismo (AoEs por sus siglas en inglés) utilizando riqueza, GIE y PAE. Atropatene es la provincial iraní más rica en endemismos de *Astragalus*. La mayoría de las áreas de endemismo se localizan en los hábitats montañosos como Alborz y Khorassan-Kopet Dagh así como en las zonas altas del sur y centro de Irán. Nuestros hallazgos muestran que las montañas juegan un papel importante en los patrones de endemicidad del género *Astragalus*, pero las llanuras, marismas y pastos también contienen numerosos endemismos y por tanto deben ser incluidos en el esfuerzo de conservación. Los resultados obtenidos a partir de las tres aproximaciones son consistentes entre ellas. Sin embargo, parece que la aproximación PAE ha sido más exitosa que los otros dos métodos y cubren la

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mayoría de las áreas de endemismo de Astragalus en Irán. Finalmente, sugerimos que, en los análisis biogeográficos en Irán, se utilicen conjuntamente técnicas basadas en mallas de celdas y aproximaciones de vecindad circular para determinar las áreas prioritarias de conservación.

Palabras clave: biogeografía; endemismo; Fabaceae; PAE; riqueza de especies.

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INTRODUCTION
Areas of endemism (AoEs) are considered the basic units for historical biogeographic studies as well as for identifying priority areas for biodiversity conservation (Fjeldså, 1993; Myers et al., 2000; Crisci et al., 2003; Lamoreux et al., 2006; Gomes-da-Silva et al., 2017). Endemism is the state of a taxon that is restricted to a particular geographical location (Anderson, 1994). AoEs harbor endemic taxa and are indicative of the evolutionary history of flora in each geographical area (Morrone, 2008). They are identified by two or taxa more co-occurring in the same area and represent a common biogeographic history and paleo-ecological events (Szumik & Goloboff, 2004; Morrone, 2008). Therefore, recognizing and delimiting the areas of endemism has always been an important and interesting topic for biogeographers and conservation biologists (Axelius, 1991; Laffan & Crisp, 2003; Jetz et al., 2004; Feng et al., 2016). To date, different methods for identifying areas of endemism have been described, including parsimony analysis of endemism (PAE) using grids (Morrone, 1994), cladistic analysis of distributions and endemism (CADE) (Porzecanski & Cracraft, 2005), endemicity analysis (EA) (Szumik et al., 2002), analysis of biotic elements (BE) (Hausdorf & Hennig, 2003), categorical analysis of neo- and paleo-endemism (CANAPE) (Mishler et al., 2014), and analysis of geographical interpolation endemism (GIE) (Oliveira et al., 2015). Previously, these approaches have been used as influential methods for mapping the centers of endemism (CoEs) and areas of endemism (AoEs) of many taxa worldwide.

The study area is Iran, one of the major biodiversity hotspots in the Middle East. The Iranian ecosystems are home to 8000 to 8112 species of plants, of which 2597 are endemic (Noroozi et al., 2019). The most important reasons for Iran’s high plant diversity are geographical isolation, climatological and edaphic differences throughout the territory, and vegetation history (Hedge & Wendelbo, 1978; Frey & Probst, 1986). Iran is known as one of the centers of endemism and speciation of many plant genera such as Astragalus L. (Fabaceae), Allium L. (Amaryllidaceae), Cousinia Cass. (Asteraceae), Acantholimon Boiss. (Plumbaginaceae), and Onosma L. (Boraginaceae) in the world (Maassoumi, 1993, 1998, 2000, 2003, 2005; Assadi, 2006; Fritsch & Abbasi, 2013; Khajoei Nasab & Mehrabian, 2022). The genus Astragalus (Fabaceae) is the biggest among flowering plant genera (Frodin, 2004). There are about 2748 species in 155 distinct sections in the Old World. Most of the endemic species in Southwest Asia are restricted to Iran with 885 species and 589 endemic species, Afghanistan with 319 species and 144 endemic species, and Turkey with 435 species and 257 endemic species. In total, in these three countries there are about 1459 taxa with 1021 endemics, which means the highest rate of endemism and is the main center of speciation in the Old World. Previous studies have investigated the geographic distribution patterns and species richness of Astragalus in Iran (Maassoumi, 1993; Mahmoodi et al., 2009, 2012; Bagheri et al., 2019; Maassoumi & Ashouri, 2022), but unfortunately, no comprehensive studies have been performed to identify areas of endemism using multiple GIS-based approaches. Hence, AoEs of this genus in Iran are not well known and they need to be accurately assessed using modern techniques. The present study aims to identify spatial endemism patterns of Astragalus in Iran using GIS-based
mapping. Therefore, the main objectives of this study are: (1) identifying the hotspots of species richness of Astragalus species endemic to Iran; (2) estimating the number of Astragalus endemics per phytogeographical province and province of the country; and (3) delimiting AoEs in the study area using PAE and GIE approaches.

MATERIALS AND METHODS

Description of the study area

The area studied (Fig. 1) is Iran, located in southwestern Asia between latitudes of 24° and 40° N and longitudes of 44° and 64° E. Iran, with a total land area of 1.6 million km², is geographically located between Central Asia, the Arabian Peninsula, the Indian subcontinent, and Europe. It is a mountainous country occupying a central position in the Mesozoic-Cenozoic Neotethyan orogenic belt (Richards & Sholeh, 2016). The geological structure of Iran is complex and highly influenced by the development and history of the Tethyan region (Stöcklin, 1974). Iran consists of various massifs such as the Alborz, Zagros, Kopet-Dagh, and Central and Eastern mountain ranges. The area has a diverse topography and elevation ranges vary from 26 m below Caspian Sea level to 5671 m at Mount Damavand. Furthermore, Iran lies within the arid and desert belt of the world, and its climate varies from hot and dry deserts in the central zone of Iran (with an average annual rainfall of less than 25 mm) to the sub-tropical humid climate on some coastlands of the Caspian Sea (with an average annual rainfall greater than 1800 mm) (Shakoor et al., 2010; Ghorbani, 2013).

Astragalus distributional data

2000, 2003, 2005, 2014), *Flora Iranica* (Podlech, 1999; Zarre et al., 2008; Podlech et al., 2010), and occurrence data from the herbarium records from IRAN, W, TUH, TARI, FUM, G-Boiss, P, MSB, L, and K herbaria (acronyms according to Thiers, 2021). In addition, the distributional data of the recent literature was added to the *Astragalus* endemics dataset (Bagheri et al., 2014, 2017; Bidarlordi et al., 2016; Bagueri & Maassoumi, 2019; Pahlevani et al., 2020; Mehrnia & Maassoumi, 2021). In total of 4180 spatial distribution records for 589 species of *Astragalus* endemic to Iran were collected.

**Richness of endemic species**

Species richness represents a simple measure of species diversity in biological conservation studies, and it is widely used to determine the conservation value of areas or habitats (Coesel, 2001). It is the number of species in a particular area or place. Species richness mapping can be performed using circular areas, circular neighborhoods, or grid cells (Hijmans & Spooner, 2001; Hijmans et al., 2002). In this study, endemic species richness was mapped using the circular neighborhood point-to-grid analysis tool based on 10 × 10 km grid cells with a 25 km radius. The circular neighborhood methods are used to eliminate boundary effects caused by grid origin assignment and reduce sensitivity to small changes in coordinate data and to achieve a smoother surface (Hijman & Spooner, 2001; Oliveira et al., 2015). DIVA-GIS v7.3 was used to create the map.

**Geographical Interpolation of Endemism (GIE)**

Geographical interpolation of endemism (GIE) includes circular neighborhood methods, and it was initially proposed and implemented by Oliveira et al. (2015). This method identifies the areas of endemism by estimating the overlap between species distributions through a kernel interpolation of the centroids of species distributions (Oliveira et al., 2015). In this study, species data were classified into one group. Since the distance between the centroid and the farthest occurrence of each species is less than 12 km and the distances of many species were close and similar, we grouped the species into a single class. Therefore, areas of endemism were identified and mapped using the GIE method and the kernel interpolation function in ArcGIS v10.3.

**Parsimony Analysis of Endemicity (PAE)**

The endemism patterns in the genus *Astragalus* were explored using parsimony analysis of endemicity (PAE). This method was originally proposed by Rosen (1984, 1985) and developed by Rosen (1988) and Rosen & Smith (1988) as a tool to evaluate the distribution of taxa in the biogeographical assemblages. Morrone (1994) modified the original PAE analysis by using a system of quadrants as the unit of analysis to delineate areas of endemism. PAE identifies areas of endemism based on a parsimonious algorithm that analyses grid cells as operational units (analogous to taxa) and classifies them according to their shared taxa (analogous to characters). First, the study area was divided into 201 cells of 1 × 1° (∼100 × 100 km²) (Appendix 1). Then, grids that did not meet the PAE standards were excluded from the matrix. Finally, to perform the PAE analysis, we constructed the presence/absence matrix of endemic *Astragalus* species on a grid of 139 1 × 1° cells. Species found in a single cell or in all cells are referred to as uninformative taxa and should be excluded from the analysis (Espadas-Manrique et al., 2003). Finally, a presence/absence matrix with 337 endemic species and 139 cells was created for PAE analysis (Appendix 2). A hypothetical outgroup without all taxa was used to root the cladogram (Morrone, 1994, 2014). The matrix was analyzed using the heuristic search option in the PAUP* v4.0a169 (Swofford, 2002), which is based on a random-addition sequences and the TBR Branch Swapping. Relative support for each branch was estimated using bootstrap analysis with 1000 reps. Finally, the areas of endemicism were localized and mapped by grid groups of the same clade sharing at least two taxa (Huang et al., 2008).

**RESULTS**

**Distribution patterns of *Astragalus* endemics in phytogeographical provinces of Iran**

In this study, the geographical distribution of endemic *Astragalus* species in Iran’s phytogeographic provinces was recognized based on the Assadi’s
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delineation of Iranian phytochoria (Assadi, 2006) (Appendix 3). According to this, endemic species of the genus were found in three regions (Irano-Turanian, Saharo-Sindian, and Euro-Siberian) and all eight phytogeographic provinces (Appendix 3). The provinces of Atropatanean and N. Balochistan had the highest and lowest numbers of endemic *Astragalus* species in Iran, respectively. Furthermore, about 58% of all endemic species (341 species) were distributed within a single phytogeographical province (Fig. 2). Among the species studied, *A. trachyacanthos* Fisch. and *A. albispinus* Sirj. & Borm. had the widest distributions and were found in six provinces (Appendix 3). Surprisingly, among the 589 endemic species, there were about 248 endemic species with one collection (type specimen), or 2–3 occurrences in very limited areas around type localities, and there were 341 endemic species with large distribution patterns. Figure 3 illustrated the richness map of *Astragalus* endemic species to provinces of Iran. Based on this map, provinces of Esfahan, Fars, and East Azarbaijan were the major hotspots of richness in Iran. Overall, the richness of *Astragalus* endemics was very diverse among provinces of Iran (Fig. 3). Esfahan (*n* = 114) and Bushehr (*n* = 5) were the provinces with the highest and lowest species numbers, respectively (Fig. 3). Also, in the two provinces of Ilam and South Khorasan, the number of species was the lowest, less than 10.

**Hotspots of species richness based the circular neighborhood point-to-grid analysis**

The circular neighborhood point-to-grid richness map was divided into five groups from 1 to 113 species, which showed that the highest number of endemic species occurred in the three hotspots of the Alborzian and Zagrosian ecosystems (Fig. 4). The first hotspot occurred in the central Alborz region between the provinces of Alborz, Tehran, and Mazandaran. There was the second major center of endemic richness between Zanjan, Qazvin, Hamedan, and Kurdistan provinces. Most of this hotspot covered Zanjan province, a rich floristic place in Iran. Zanjan is known as a mountainous province whose important mountain ranges, such as the Belqis and Qeydar mountains, are home to many local endemic species of *Astragalus* such as *A. abharensis* Maassoumi & Podlech, *A. anguranensis* Podlech & Maassoumi, *A. austromahneshanensis* F. Ghahrem., Maass. & Bagheri, *A. belghelisicoides* Podlech & Maassoumi, *A. belghelisicus* Maassoumi, *A. zanjanensis* Podlech & Maassoumi, etc. The third hotspot occurred in parts of the provinces of Esfahan, Lorestan, Markazi and Chaharmahal and Bakhtiari (Fig. 4). Therefore, these three major hotspots included the most endemic species of *Astragalus* in Iran (91–113 spp.).

![Figure 2](https://example.com/figure2.png)

**Figure 2.** Numbers of *Astragalus* endemics present in one or more phytogeographical provinces of Iran

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Figure 3. Species richness map of Astragalus endemics in provinces of Iran.

Figure 4. Species richness map of Astragalus endemics to Iran based the circular neighborhood point-to-grid richness.
Areas of endemism (AOEs) based on the GIE method

In total, seven areas of endemism for *Astragalus* were identified using the GIE method in Iran, which had the highest Kernel index (Fig. 5). According to this map, most of these areas were in Iran’s major highland ecosystems. **AoE1** was in the Khorassan-Kopet Dagh floristic province in northeastern Iran. This area was one of the areas of endemism of the genus under investigation, which included many endemic species, especially local endemics, including *A. austrokhorasanicus* Podlech, *A. baharensis* F. Ghahrem., *A. bajgiranensis* Podlech, *A. zoshkensis* F. Ghahrem., etc. (Fig. 6). **AoE2** occupied most of the central Alborz region. The region was in the provinces of Alborz, Tehran, and Mazandaran. **AoE3** was located at the intersection of the Alborz, Zagros and Azerbaijan Plateaus and included the provinces of Zanjan, Qazvin, Hamedan, Lorestan, Markazi, Ilam, Kermanshah, and Kurdistan (Fig. 6). In addition, the study identified the Atropatanean province or plateaus of Azerbaijan as another area of endemism (**AoE4**). In this area, narrow and local endemic species were widely distributed, such as *A. aharicus* Maassoumi & Podlech, *A. birangae* Maassoumi, *A. doghrunensis* Maassoumi & Podlech, *A. kaleibarensis* Podlech, *A. kiamaky-daghensis* Maassoumi & Podlech, etc. (Fig. 7). **AoE5** was mainly found in the Zagros Mountains, especially in the central and southern Zagros Mountains, and in the central mountains of Iran, such as the Shirkuh and Karkas Mountains. The **AoE2**, **AoE3**, and **AoE5** identified by GIE were in good agreement with the three hotspots of endemic richness mentioned above. **AoE6** was located on Mount Hezar and Mount Lalezar in the southern parts of Iran. Finally, the Taftan Mountain in southeastern Iran was the site of the **AoE7** (Fig. 5).

![Figure 5. Areas of endemism of *Astragalus* in Iran, identified using GIE.](https://example.com/image-url)
Areas of Endemism (AOEs) based on the PAE analysis

Analysis of the data matrix yielded 20,000 cladograms with a length of 1219 steps, a consistency index (CI) = 0.276, and a retention index (RI) = 0.402. The strict consensus cladogram was largely unresolved and showed a polytomy composed of 139 grid cells (Fig. 8). The tree showed four main clades representing major areas of endemism (AoEs) (Fig. 9). AoE1 included parts of north-western Iran, most of the habitats of Zagros, some parts of the central mountains in Yazd province, and parts of Sistan and Baluchistan, Kerman, and Hormozgan provinces in southern Iran. AoE2 was mainly concentrated in the northern, northeastern, and northwestern parts of Iran. Part of the western part of the country (Kermanshah) and a limited area of Kerman, and Sistan and Baluchistan were also located in this area. AoE3 was scattered throughout Iran and was in parts of the northeast, northwest, center, southwest and southeast. The main part of AoE4 was in the eastern, northeastern, and southeastern parts of the country, and a limited part of northern, western, and central Iran.

DISCUSSION

This is one of the first detailed studies to identify the areas of endemism and hotspots of the endemic richness of Astragalus in Iran. According to our results, Esfahan province had the highest numbers of endemic Astragalus species in the country. This province with 201 species belonging to 42 Astragalus sections is one of the important centers of diversity and speciation of this genus in Iran (Mahmoodi et al., 2012; Akhavan Roofigar et al., 2019). Due to its geographic location, the presence of important mountain ranges such as

Figure 6. Some endemic species of Astragalus in N. Khorasan province: (A), A. edmondonii, Kurdo-Zagrosian province; (B), A. megalotropis; (C), A. microphysa; (D), A. rhabdophorus.
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Figure 7. Some endemic species of *Astragalus* in Atropatanean province: (A), *A. chrysostachys*; (B), *A. jodotropis*; (C), *A. stenolepis*; (D), *A. pereshkhoranicus*.

the Zagros Mountains and Karkas Mountains, and the various predominant climatic zones, the number of endemic species is highest. The province of Esfahan is also located between the Kurdo-Zagrosian and Central Iran provinces, so the combination of these factors makes it a suitable place for the richness of *Astragalus* endemics. In addition, Atropatanean had the highest endemic richness among the phytogeographical provinces of Iran. Atropatanean is an important center of Iran’s plant diversity and endemism (Assadi, 2006; Noroozi et al., 2018; Khajoei Nasab & Khosravi, 2020; Khajoei Nasab & Mehrabian, 2022). Most parts of the area cover northwest Iran at the intersection of the Alborz, Zagros, and the Caucasus Mountains. The collision of these mountains and the presence of two different climatic zones (Dajmali et al., 2011) have created habitats suitable for many endemic *Astragalus* species, especially local and narrow endemic species. Previous phytogeographical studies by Mahmoodi et al. (2009, 2012) identified the province as one of the important centers of endemism of this genus in Iran.

On the other hand, the three hotspots of species richness were identified by the circular neighborhood method. The first hotspot was in the Alborz ecosystems (in the central Alborz region). The Alborz Mountains have formed a heterogeneous macroecosystem for the diversity and endemicity of many plant groups such as *Astragalus*, *Acantholimon*, *Onosma*, etc. (Hedge & Wendlbo, 1978; Noroozi et al., 2008, 2018; Khajoei Nasab & Khosravi, 2020). The second hotspot was located at the confluence of the Alborz and Zagros Mountain ranges and the Azerbaijan plateau. The existence of a cold and mountainous climate along with different soil compositions and specific topography has provided the conditions for the high endemic species richness of this genus in this region. The third hotspot was in the central Zagros, a place that has become
Figure 8. Strict consensus cladogram obtained PAE analysis for Astragalus and “x” represents the hypothetical outgroup area.
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Figure 9. Four areas of endemism (AoEs) for *Astragalus* in Iran identified by PAE analysis.

Using GIE, seven AoEs were identified in Iran based on spatial data of the endemic *Astragalus* species. AoE1 was in the Khorassan-Kopet Dagh floristic province in the northeast of Iran. This area well corresponds to the distribution pattern of Khorassan endemism of the montane/alpine regions of the Irano-Turanian region (Hedge & Wendlbo, 1978), N. Khorassan (Assadi, 2006) as well as the endemic patterns of *Acantholimon* (Khajoei Nasab & Khosravi, 2020). Khorassan-Kopet Dagh is in a transitional position between the different phytogeographical geographical units of the Irano-Turanian and Euro-Siberian regions, which makes it a major area of endemism and diversity of plant species in Iran. AoE6 was located in the Hezar and Lalezar mountains in the Kerman province. These high mountains of the Yazd–Kerman massif are parts of the Irano-Turanian region, which include an ecotone zone on its southern border to the Saharo-Sindian region and provide habitats suitable for...
many endemic species of many plant genera such as *Astragalus*, *Echinops* L., *Cousinia*, *Acantholimon*, *Nepeta* L., etc. (Zohary, 1973; Léonard, 1981; Doostmohammadi et al., 2018; Noroozi et al., 2018; Khajoei Nasab & Khozravi, 2020; Khajoei Nasab et al., 2022). Finally, Mount Taftan in southeastern Iran is home to several endemic species of *Astragalus*. This mountain has provided a suitable place for the growth of mountain species endemic to southern Iran. Therefore, it could be concluded that mountain ranges play an important role in the diversity and endemism of different plant species in Iran.

According to the results of the PAE analysis, 87% of the total area of can be considered as the areas of endemism (AoEs) of the genus *Astragalus*. This suggests that in addition to highland ecosystems, the plains and lowlands are also important areas of endemism of *Astragalus* in Iran, so its AoEs are not limited to the highlands. A recent study of the distribution patterns of *Astragalus* confirms the existence of high species richness of some sections (i.e. *Leucocercis*, *Bucerales*, *Eremophysea*, *Ammodendron*) in the plains, salt marshes, and lowlands of Iran (Mahmoodi et al., 2012). Large parts of the four AoEs detected in this study were in the prominent mountains of Iran, which is consistent with previous studies in Iran (Hedge & Wendelbo, 1978; Assadi, 2006; Mahmoodi et al., 2012; Mehrabian, 2015; Bagheri & Maassoumi, 2019; Noroozi et al., 2019; Khajoei Nasab & Khozravi, 2020; Mehrabian et al., 2021). The northern and western mountains of Iran, i.e. Alborz and Zagros, are among the Irano-Anatolian biodiversity hotspots and are known to be the 20th global hotspot area (Myers et al., 2000; Mittermeier et al., 2005).

**CONCLUSIONS**

Endemism patterns of *Astragalus* in Iran were analyzed by identifying hotspots of richness and AoEs. We found that identifying endemism patterns using multiple approaches such as PAE, GIE, and species richness could outperform one approach to identify centers with conservation priority. The results of the three approaches were in good agreement with each other. However, it seems that PAE has been able to operate much more successfully than the other two approaches and cover more the areas of endemism of this genus in Iran. Thus, this study shows that the pattern of endemism of plant taxa in Iran does not follow the same pattern, and that the center of speciation and endemism of all plant groups does not occur only in the mountains. Mountains play an important role in endemism, but plains and rangelands are also home to many endemic species, so they should be prioritized. As these areas are more at risk of extinction due to destructive human activities such as overgrazing, fires, and droughts, as well as climate change, it is important to determine a strategy to protect most of the areas identified in this study.

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**REFERENCES**


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**APPENDICES**

Appendices 1 to 3, due to their size, are available for download online in the HTML version of the article.