Evaluating the effectiveness of vegetation conservation on a sacred mountain in western China

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Academic editor: Ji-Zhong Wan | Received 28 July 2021 | Accepted 24 October 2021 | Published 26 November 2021

http://zoobank.org/0FCE3073-F3DA-4929-8578-3F340A24F979

Citation: Cao Z, Dou L, Yang N, Zhang K, Wang B, Xu Y, Ran J (2021) Evaluating the effectiveness of vegetation conservation on a sacred mountain in western China. Nature Conservation 45: 1–9. https://doi.org/10.3897/natureconservation.45.72215

Abstract
Sacred natural sites, as probably the oldest form of habitat reserve for religious or cultural causes worldwide, are suggested to have an important role in conserving vegetation; however, there are insufficient data supporting the detailed implications of such sites for vegetation conservation. Thus, we evaluated the effectiveness of vegetation conservation on a Tibetan sacred mountain in Yajiang County, Sichuan, China, by investigating species richness and the structural attributes of higher vascular plant communities on and around the sacred mountain from April to June 2009. The results showed that the number of tree species on the sacred mountain was significantly higher than that in the surrounding area, but there were no notable differences in the numbers of shrub and grass species between the two sites. The sacred mountain harbored a greater number of small, short trees compared with the surrounding area, wherein the low-shrub and grass understory was relatively dense. We conclude that the sacred mountain has a positive impact on indigenous vegetation protection, but disparities in the management of the allowed uses of such sites could reduce their conservation effectiveness.

Keywords
Forest conservation, indigenous communities, richness, sacred natural site, vegetation structure

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Introduction

There are numerous ethnic groups across the world, which have existed for centuries, for the most part from ancient times (Dudley et al. 2005). Many such groups define forests or mountains as sacred areas, protecting such regions for religious or cultural reasons, because they believe that everything has a soul, with some areas having resident deities or spirits. Access to sacred natural sites is usually restricted, and logging is forbidden (Colding and Folke 2001). Thus, sacred natural sites are suggested to be beneficial to vegetation conservation (Bhagwat and Rutte 2006).

Some research has indicated a higher plant diversity in sacred sites compared with open-access sites. For example, Gawade et al. (2018) suggested that sacred groves harbored more threatened and rare plant species relative to associated surrounding plots in Dapoli Taluka, India. Aerts et al. (2016) reported more indigenous woody species owned by Ethiopian church forests compared with corresponding natural forests, while Gao et al. (2013) documented higher tree diversity in culturally protected forests than in nearby forests without cultural protection in southeast China. However, Bhagwat et al. (2005) found that the overall species richness of trees did not significantly differ among sacred groves, officially protected areas, and coffee plantations in the Western Ghats of India. In terms of vegetation attributes, Salick et al. (2007) demonstrated that sacred forests in northwest Yunnan, China preserved some characteristics of old-growth forests; Shen et al. (2015) found that Tibetan sacred mountains of cultural importance had higher forest cover than the nearby unmanaged open-access areas. Whereas, Levy-Tacher et al. (2019) found that few differences existed for structural attributes (e.g., basal area and tree height) between Mayan sacred forests and the nearby areas of mature forests. Thus, given that there are insufficient data supporting the detailed implications of sacred sites for vegetation conservation, more research is required to determine the conservation effectiveness of such sites, especially for poorly known areas (Xu et al. 2019).

In this study, we evaluated the effectiveness of vegetation conservation on a Tibetan sacred mountain in western China. By comparing higher vascular plant (i.e., seed plant) communities on and surrounding the sacred mountain, we investigated whether species richness and the structural attributes of communities differed between the sacred mountain and the surrounding area.

Methods

Study site

The study site was located in Pamuling (30°06'N, 101°11'E; Fig. 1), Yajiang County, Garzê Tibetan Autonomous, Sichuan, China, which occurs in the sub-humid climate zone of the Qinghai-Tibet Plateau. The vegetation comprises five main types: fir–larch forests (dominated by Abies squamata, and Larix potaninii), mixed spruce–larch–birch
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forests (dominated by *Picea* sp., *L. potaninii*, and *Betula platyphylla*), oak thickets (dominated exclusively by *Quercus aquifolioides*), pine forests (dominated exclusively by *Pinus densata*), and rhododendron shrubs (*Rhododendron nitidulum*, *Rh. flavoflorum*, *Salix* sp., and *Dasiphora fruticosa*). The sacred mountain covers ~20 km², ranging mainly in elevation from 3,300 to 4,200 m, and was established by a Tibetan Buddhist monastery and associated with a mountain deity (see Xu et al. 2019 for more detail). Unless for the purpose of performing Buddhist worship, people were usually restricted from accessing the sacred mountain by the assigned specific guardians in the monastery. Logging was also prohibited.

**Figure 1.** Map showing the location of the study site (black triangle) and sampling points (white dots) on and surrounding the sacred mountain.
The area surrounding the sacred mountain was accessible. The woodlands in the surrounding area were under threat from cutting by the local communities for cooking and heating, despite a national logging ban imposed on natural forests in the upper reaches of the Yangtze River in 1998 (Xu et al. 2016). For comparison with the sacred mountain site, we delimited a range of ~30 km² surrounding the mountain, which ranges in elevation from ~3,300 m to ~4,300 m and has similar topographical features to the sacred mountain.

Measurement of species richness and community structural attributes

We conducted fieldwork to measure species richness and the structural attributes of higher vascular plant communities (including tree, shrub and grass layers; see Table 1) between April and June 2009. We positioned sample points approximately every 250 m along ten transects of 0.3–5 km established centered on the monastery and its associated mountain deity. We positioned 37 sampling points on the sacred mountain, and 47 sampling points in the surrounding area (Fig. 1). At each sampling point, we established one 10 × 10 m plot to record the number of tree species. Based on Di Gregorio (2005) and Ravindranath and Ostwald (2008), we categorized trees into three size groups: (1) small [diameter at breast height (DBH) < 10 cm], (2) medium (10 cm ≤ DBH < 30 cm), and (3) large trees (DBH ≥ 30 cm), and into two height groups: (1) short (< 5 m), and tall (≥ 5 m) trees. We recorded the number of trees of different size groups and following the method introduced by Prodon and Lebreton (1981), we visually estimated coverage of trees of different height groups. We divided the 10 × 10 m plot into four 5 × 5 m plots. We recorded the cumulative number of shrub species in the four 5 × 5 m plots. We visually estimated coverage of shrubs with height < 1.5 m and ≥ 1.5 m in each 5 × 5 m plot, respectively, and averaged the coverage values in the plots. We further nested five 1 × 1 m sub-plots (four set in the center of each of the four 5 × 5 m plots, respectively and one the center of the 10 × 10 m plot), by a five-point sampling method (Zhang 1995). We recorded the cumulative number grass species in the five 1 × 1 m sub-plots. We visually estimated grass coverage in each 1 × 1 m sub-plot, and averaged the coverage values in the sub-plots.

Statistical analysis

We used multivariate analysis of variance (MANOVA) to examine the differences in richness of tree, shrub and grass species between the sacred mountain and its surrounding area. We used principal component analysis (PCA) on structural attributes measured between the two sites to identify the most prominent gradients, and examined their differences using permutational multivariate analysis of variance (PERMANOVA). We operated the analyses on R 4.0.5 (The R Core Team 2021) with the vegan package (Oksanen et al. 2020) and visualized data with the ggplot2 package (Wickham et al. 2021). $P < 0.05$ indicated statistical significance.
Results

The number of tree species in the sacred site was significantly higher than in its surrounding area (Fig. 2A). However, there were no notable differences in the numbers of shrub (Fig. 2B) and grass species (Fig. 2C) between the two sites.

The PCA analysis (Fig. 3) yielded two principal components of community structural attributes (rendered in the form of two axes). The first axis (eigenvalue = 2.64, explaining 33.0% of the variance) represented mainly the structure of the grass and low-shrub understory and canopy, contributed positively by the coverage of grasses and shrubs < 1.5 m in height, but contributed negatively by the coverage of trees ≥ 5 m in height and the number of trees with DBH 10–30 cm. The second axis (eigenvalue = 2.02, explaining 25.3% of the variance) represented primarily the structure of the subcanopy.

Table 1. Species richness and structural attributes of higher vascular plant communities measured in the study.

| Item                              | Description                      |
|-----------------------------------|----------------------------------|
| Species richness                  |                                 |
| Number of tree species            | Counted                          |
| Number of shrub species           | Counted                          |
| Number of grass species           | Counted                          |
| Structural attributes             |                                 |
| Number of trees with DBH < 10 cm  | Counted                          |
| Number of trees with DBH 10–30 cm | Counted                          |
| Number of trees with DBH ≥ 30 cm  | Counted                          |
| Coverage of trees with height < 5 m | %, Estimated following the method proposed by Prodon and Lebreton (1981) |
| Coverage of trees with height ≥ 5 m |                                 |
| Coverage of shrubs with height < 1.5 m |                                 |
| Coverage of shrubs with height ≥ 1.5 m |                                 |
| Grass coverage                    |                                 |

Figure 2. Number of higher vascular plant species between the sacred mountain and the surrounding area A tree, B shrub and C grass. Boxplots show the median, 25th, and 75th percentiles, Tukey whiskers (median ± 1.5 × interquartile range). ***, $P < 0.001$; NS., $P > 0.05$. 
and high-shrub understory, contributed positively by the number of trees with DBH ≥ 30 cm, negatively by the number of trees with a DBH < 10 cm, and the coverage of trees < 5 m in height and by shrubs ≥1.5 m in height. Although there was a large overlap between the two ellipses where most of the sample sites on both the sacred and its surrounding area were located, PERMANOVA testing indicated a prominent difference in the structural attributes between the two sites, which can be represented by the two significantly separated sections in the lower left corner of the ellipse of the sacred site and the right side of the ellipse of the surrounding area (Fig. 3). The separation indicated that the sacred mountain harbored a greater number of small, short trees compared with its surrounding area, where the low-shrub and grass understory was denser.

**Figure 3.** Multivariate principal component analysis (PCA) of the structural attributes of higher vascular plant communities. The triangle and round points, with 95% density ellipses, represent the sacred mountain and its surrounding area, respectively. Abbreviations: treeH1, number of trees with DBH < 10 cm; treeH2, number of trees with DBH 10–30 cm; treeH3, number of trees with DBH ≥ 30 cm; treeC1, coverage of trees with height ≥ 5 m; treeC2, coverage of trees with height < 5 m; shrubC1, coverage of shrubs with height < 1.5 m; shrubC2, coverage of shrubs with height ≥ 1.5 m; grassC, grass coverage.
Discussion

This study investigated the differences in species richness and the structural attributes of higher vascular plant communities between a Tibetan sacred mountain and its surrounding area. The results showed that the sacred mountain maintained a higher number of tree species than the surrounding area, which is consistent with many previous studies on sacred natural sites (Salick et al. 2007; Gao et al. 2013; Aerts et al. 2016; Levy-Tacher et al. 2019). There was a prominent difference in structural attributes between the two sites. The sacred mountain harbored a greater number of small, short trees compared with the surrounding area, whereas low-shrub and grass understory in the surrounding area was relatively dense. In the range of our study site, local people generally harvested trees that were both short and small in diameter, such as *Q. aquifoloides* for fuel, despite a national logging ban imposed on natural forests (Xu et al. 2016). For specific religious and cultural beliefs, local people were not allowed to enter the sacred mountain to cut trees. As a result, trees were more species rich, and the layers of small trees were denser on the sacred mountain than in its surrounding area.

However, we did not find a significantly higher richness of shrub and grass species on the sacred mountain compared with its surrounding area. Previous studies (e.g., Salick et al. 2007; Gao et al. 2013) documented similar results and suggested that they might be the result of the forms of anthropogenic use allowed in a sacred site. In the study site, trees, rather than shrubs or grasses, were commonly considered sacred by the local community, as reported in other sacred sites (Bhagwat and Rutte 2006). Although the use of forest resources, especially of trees, was restricted on the sacred mountain, collection of medicinal and other non-timber plants and grazing were allowed to some extent. This might explain why there was no significant difference in the richness of shrub and grass species between the sacred mountain and the surrounding area.

Nevertheless, the coverage of shrubs < 1.5 m in height and grasses was obviously less on the sacred mountain than in the surrounding area. This might be the result of allelopathy (Zhang et al. 2021) and the shadow effect (Jennings et al. 1999; Guo et al. 2003). The dense tree layer on the sacred mountain might severely restrict the germination of seeds, growth of seedlings, and regeneration of low shrubs and grasses. By contrary, the renewal of low-shrub and grass layers was promoted in the surrounding area where the coverage and number of small trees was both relatively low.

In conclusion, this study revealed the effectiveness of vegetation conservation on a Tibetan sacred mountain in western China. In terms of access and utilization, such sites can complement officially protected areas. However, ‘sacred’ might be a relative term, given disparities in the management of allowed uses of resources such as trees, shrubs, and grasses. Therefore, conservation knowledge based on community ecology should be introduced to indigenous communities. In addition, the sacredness of a site might mean more to local peoples than to outsiders (Shen et al. 2015). Tourism based on the Tibetan traditional culture and customs has flourished in recent years, along with the rapid development of road construction in western China (Brandt et al. 2012). Tourists often tend to disturb these sites and the relative lack of restrictions could threaten cultural assets and even modes of life. Hence, we suggest additional leg-
islative protection with strict restrictions for the activities of local people and tourists, to help protect these important conservation areas.

Acknowledgements
We thank the Forestry Bureau of Yajiang County and Pamuling Monastery for permission and support for the fieldwork. We thank two reviewers for their valuable comments on the manuscript. This work was supported by the Joint Fund of the National Natural Science Foundation of China and the Karst Science Research Center of Guizhou Province (grant number U1812401); Guizhou Provincial Department of Science and Technology-Guizhou Normal University Joint Fund Project (grant number LH [2017] 7369); and Doctoral Foundation of Guizhou Normal University (grant number 2016).

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Abstract
The global loss of biodiversity is a pressing and urgent issue and halting loss is the focus of many international agreements and targets. However, data on species distribution, threats and protection are limited and sometimes lacking in many parts of the world. The British Virgin Islands (BVI), part of the Puerto Rican Bank Floristic Region in the Caribbean Biodiversity Hotspot, is rich in plant diversity and regional endemism. Despite the established network of National Parks in the BVI and decades of botanical data from international collaboration between the Royal Botanic Gardens, Kew and the National Parks Trust of the Virgin Islands, there was a need for consolidated data on species distribution across the archipelago and national lists for threatened and rare plants of conservation concern. The process of identifying the network of 18 Tropical Important Plant Areas (TIPAs) in the BVI, completed in 2018, delivered national lists and accurate data for all 35 Species of Conservation Concern. These data (3688 georeferenced records) are analysed here to reveal species distribution across the archipelago, within the TIPAs network and the National Parks System. The TIPAs network contained all 35 Species of Conservation Concern and 91% of all the records, as expected. Ten out of the 21 National Parks had one or more of the species present. Most species occur across the archipelago, while some are restricted range and/or endemics. These new data will help management of
Introduction

Nature is declining at an unprecedented rate and global wildlife populations have decreased by 68% since 1970 (WWF 2020). Estimates of global extinction rates are 100–1000× greater than in the geological past (Dasgupta 2021). The landmark report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) estimated that up to one million species may be threatened with extinction (IPBES 2019). Recent analyses have estimated that 2 in 5 plants are threatened with extinction with habitat loss due to agricultural expansion being the greatest single threat (Nic Lughadha et al. 2020). The global climate emergency (Ripple et al. 2020) is adding greater pressure to already vulnerable species and habitats (IPCC 2014). Conservation biologists are in a race against time to identify the most important areas of the world for wild species diversity and to focus resources towards protecting these sites. As we better understand that our economies, livelihoods and well-being all depend on Nature, there is greater support from the wider population for increased and urgent conservation interventions (Dasgupta 2021). Developing priorities for these conservation interventions has been the focus of much research targeting regional scale sites, such as Biodiversity Hotspots (Mittermeier et al. 1998; Myers et al. 2000) or discrete sites, such as Alliance for Zero Extinction sites (Ricketts et al. 2005). Other approaches target specific groups of taxa, such as Important Bird Areas (IBAs) (Donald et al. 2019) or concentrations of multiple taxa, such as Key Biodiversity Areas (KBAs) (KBA 2020). For plants, identifying Important Plant Areas (IPAs) (Darbyshire et al. 2017; Plantlife 2018), particularly in the tropics, has become an area of increased activity and the application of this methodology is the focus of this paper.

The Caribbean Region is estimated to contain 12% of the plant diversity and 29% of the medicinal plants (spermatophytes only) of the Americas in only 1% of the land area (IPBES 2018). The Puerto Rican Bank Floristic Region comprising the British Virgin Islands (BVI), the United States Virgin Islands (USVI) and the Commonwealth of Puerto Rico, is located in the Caribbean Biodiversity Hotspot (Myers et al. 2000) and has a diverse flora with 2,108 native taxa, of which 292 are regional endemics (Lugo et al. 2006; Acevedo-Rodríguez and Strong 2012). This endemism is partly explained by most of the floristic region previously being one landmass during the Last Glacial Maximum when sea levels were much lower (Lambeck et al. 2002; Renken et al. 2002; Siddall et al. 2003; Mann et al. 2005; Hamilton 2016) and the Caribbean proximity to South America, Mesoamerica and North America (Santiago-Valentin and Olmstead 2004; Acevedo-Rodríguez and Strong 2008). The
BVI itself is a tropical archipelago with a land mass of 153 km² with approximately 50 rocks, keys and islands and a native flora of 648 vascular seed plants, including four endemic taxa: *Vachellia anegadensis* (Britton) Seigler & Ebinger, *Metastelma anegadense* Britton, *Pitcairnia jareckii* Proctor & Cedeño-Mald. and *Senna polyphylla* var. *neglecta* H.S. Irwin & Barneby (Acevedo-Rodríguez and Strong 2012; The BVI TIPAs National Team 2019b).

Identifying species diversity and distribution is key to protection and prevention of biodiversity loss at a global and local scale, as robust data are paramount for well-informed decisions on policy, conservation and species management. However, it is important not only to identify which plant species occur in an area, but also their vulnerability to threats (e.g. loss of habitat, invasive species, pests), protection (e.g. protected areas, legal status) and conservation importance (e.g. endemic species, keystone species) to reduce loss of biodiversity and protect global biodiversity hotspots (Mittermeier et al. 2011). Extinction risk assessments, particularly of endemic species, are an important tool for prioritising conservation efforts and preventing biodiversity loss (Nic Lughadha et al. 2020). The only Caribbean UK Overseas Territory (UKOT) with a complete National Red List is the Cayman Islands which includes 415 taxa, with 46% of them being threatened with extinction (Burton 2008). Extinction risk assessments and botanical surveys are on-going in several of the Caribbean UKOTs and countries (Clubbe et al. 2020).

IPAs consider not only species distribution and botanical richness of an area, but also prioritise those plants and habitats under threat by identifying a network of key sites for the conservation of wild plants and threatened terrestrial habitats (Plantlife 2018). The guidelines developed by Plantlife for Europe (Anderson 2002) have been tested and implemented in many countries in the past two decades, mostly temperate regions in Europe and the Mediterranean (Atay et al. 2000; Anderson et al. 2005; RBG Kew 2016; Darbyshire et al. 2017; Willis 2017; Plantlife 2018). IPAs are key to Target 5 of the Convention on Biological Diversity (CBD) Global Strategy for Plant Conservation (GSPC) which aims to protect > 75% of the most important areas for plant diversity in each ecological region in the world (Secretariat of the Convention on Biological Diversity 2012; GSPC 2021).

The focus of IPAs identification has shifted recently to the tropics following a review of the IPAs guidelines (Darbyshire et al. 2017). Tropical Important Plant Areas (TIPAs) aim to extend the network of IPAs into the most diverse regions of the world. The TIPAs process includes participatory workshops with stakeholders (e.g. government bodies, NGOs, community members), botanical surveys, data consolidation, assessments of extinction risk and vegetation mapping. The resulting data on globally threatened species and regional/national species of conservation concern and their distribution, botanically rich areas and threatened habitats help deliver a strong and scientifically-sound framework for species and habitat conservation and management. In 2019, annotated checklists of threatened plant species for the Guinea-Conakry region in Guinea (Couch et al. 2019a) and Mozambique (Darbyshire et al. 2019) were produced using the TIPAs process and the first TIPAs of Tropical Africa were
identified in Guinea (Couch et al. 2019b). An endemic species list for the Ebo Forest in Cameroon, a proposed National Park, have been published during the TIPAs identification process, reinforcing the importance of this area for local conservation (Cheek et al. 2018). Preliminary work in the Caribbean UKOTs of the British Virgin Islands, the Turks and Caicos Islands and Montserrat, identified candidate sites for IPAs, but more extensive botanical surveys and a framework were needed to progress and complete a network of IPAs for these countries (Clubbe et al. 2020).

Despite their importance, levels of legal protection of IPAs and TIPAs vary widely from nearly 100% in the UK to below 50% in parts of North Africa and the Middle East (Willis 2017). Aichi Biodiversity Target 11 highlights the importance of effective and equitably managed protected areas as an important management tool to conserve biodiversity (CBD 2011). However, data on globally and nationally threatened species and habitats are not always available to assess biodiversity within protected areas (Watson et al. 2014). The BVI Protected Areas System Plan 2007–2017 (Gardner et al. 2008) concerns the established network of protected areas across the archipelago. However, the majority of these areas have been chosen, based on the ecosystem services they provide and fauna diversity, for example, watersheds, nesting sites for migratory birds, as only limited information on the flora was available at the time (Smith-Abbott et al. 2002; Pascoe et al. 2015).

This work complements the TIPAs process in the BVI and previous botanical research by presenting and analysing species richness and distribution of the Species of Conservation Concern and globally threatened species across the archipelago using all available high resolution botanical data. For the first time, species representation within the BVI TIPAs and National Parks are discussed and gaps in in situ conservation identified. Further, we discuss the implications of these findings to future species management, plant conservation and policy in the BVI. These findings have implications for the wider Caribbean Region.

**Methods**

**Botanical data and species of conservation concern (SCC)**

A target list of priority native plant species was compiled using baseline data from: 1) two decades of botanical work in the BVI by the National Parks Trust of the Virgin Islands (NPTVI); Royal Botanic Gardens, Kew, UK (Kew); and regional partners; 2) previous Red Listing work (Pollard and Clubbe 2003) and 3) botanical literature for the Puerto Rican Bank (Grisebach 1859; Eggers 1879; Urban 1898; Britton 1918; D’Arby 1967, 1975; Little et al. 1976; Acevedo-Rodríguez 1996; Axelrod 2011), especially the ‘Catalogue of Seed Plants of the West Indies’ (Acevedo-Rodríguez and Strong 2012). The target list included species present in the BVI and in one or more of the following categories: a) globally threatened species included in the 2018 International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN
BVI TIPAs, plant species richness and conservation

2018), b) endemic to the Puerto Rican Bank and c) restricted range species (Bárrios et al. 2017). Globally threatened species are those in one of the threatened categories of Vulnerable (VU), Endangered (EN) or Critically Endangered (CR). Restricted range species were defined as native plants which only occur in one country/territory or region with an Extent of Occurrence (EOO) < 10,000 km², following the concepts for TIPAs by Darbyshire et al. (2017) and the IUCN KBA Standard (KBA 2020).

A total of 3,688 high accuracy (+/- 10 m) georeferenced location records for 35 of the priority species were included in this analysis. Records were retrieved from the Kew UKOTs Species and Specimens Database (SSD) (UKOTsTe am 2021), which contains a compilation of records from herbaria (e.g. Kew, MAPR, MO, NY, SJ, UPRRP, US) and data from field surveys carried out by Kew and NPTVI between 2000 and 2018 across 23 islands of the BVI. Data were checked and duplicated location records for individual plants were excluded before retrieval from the database. Data were available for terrestrial vascular seed plants only.

Extinction risk assessments and re-assessments for 30 priority species were undertaken collaboratively by experts from Kew, NPTVI, University of Puerto Rico, US Fish and Wildlife Service (USFWS) Caribbean Ecological Services Field Office (CESFO) and Puerto Rico Departmento de Recursos Naturales y Ambientales (DRNA), following the IUCN standards and criteria methodology (IUCN Standards and Petitions Committee 2017). All assessments, except two for natural hybrids, were published in the IUCN Red List of Threatened Species. Five other priority species were not reassessed due to their wide distribution.

Tropical Important Plant Areas (TIPAs)

A series of workshops involving botanical experts, local conservation practitioners, Government representatives and community members, led by Kew and NPTVI, were held in the BVI in 2016 and 2017 to introduce and apply the TIPAs methodology (Darbyshire et al. 2017; Plantlife 2018), define fieldwork priorities through gap analysis and identify priority native plant species (The BVI TIPAs National Team 2019a).

The BVI national list of Species of Conservation Concern (a.k.a. species of high conservation importance) was agreed in 2018 and used in the TIPAs process (The BVI TIPAs National Team 2019a). The Species of Conservation Concern comprise native species listed as globally threatened in the 2018 IUCN Red List of Threatened Species (IUCN 2018) or restricted range species (EOO < 10,000 km²). Species were assessed following the criteria detailed in Darbyshire et al. (2017) and applied by the BVI TIPAs national team (2019a). Globally threatened species were considered under TIPAs qualifying criterion A(i) - site contains one or more globally threatened species. Species of Conservation Concern were considered under TIPAs criteria A(iii) - site contains one or more highly restricted endemic species [EOO < 100 km²] that are potentially threatened; A(iv) - site contains one or more range restricted endemic species [EOO > 100 km² and < 5,000 km²] that are potentially threatened; and B(ii) - site contains > 10% of the species in the national list of Species of Conservation Concern.
(i.e. four species) or is one of the 15 richest sites nationally. The thresholds for the restricted endemics align, respectively, to the CR and EN categories of the IUCN Red List assessments under criterion B (IUCN Standards and Petitions Committee 2017). Additional conditions for the site to qualify under Criterion A includes being one of the five best sites nationally for the species or contain > 1% of its global population or > 5% of its national population.

The TIPAs Network for the BVI was identified and agreed in 2018. Detailed description of the TIPAs sites identified and mapped, including qualifying criteria, were published during the TIPAs process (The BVI TIPAs National Team 2019a, 2019b).

All species records were added to a bespoke Geographic Information System (GIS) project in ArcGIS Desktop software (ESRI, version 10.1, Redlands, CA, USA), containing layers for the TIPAs network and National Parks for the BVI to enable data visualisation, querying and mapping (The BVI TIPAs National Team 2019a).

National parks

The 21 declared National Parks and eight Proposed National Parks used for the analyses presented in this paper correspond to the terrestrial National Parks in the BVI Protected Areas System Plan 2007–2017 (Gardner et al. 2008). The plan includes declared marine and terrestrial protected areas managed by NPTVI and proposed new sites with various levels of protection and management. Declared National Parks are referred to as National Parks in this paper.

Results

Data and distribution of species of conservation concern across the BVI

The BVI list of Species of Conservation Concern contains 35 species, all of them previously identified as target priority species. The Species of Conservation Concern comprise the 25 species assessed as globally threatened, plus ten national endemics and/or restricted range species with qualifying EOO (Table 1). These species were used for the identification of a network of 18 TIPAs across the archipelago (Fig. 1) (The BVI TIPAs National Team 2019a, 2019b).

A total of 3,143 records were from globally threatened species. The total number of records per species varied widely from one to over 900, with most species having < 40 records and two of the species, *Vachellia anegadensis* and *Varronia rupicola* (Urb.) Britton, having > 700 records (Table 1).

Species of Conservation Concern were distributed across 23 islands of the archipelago (Fig. 2) and no single island supported all the species. The highest number of SCC and records were found in the largest islands in the BVI: Tortola (23 SCC, 256 records, total island area 57 km²), Anegada (14 SCC, 2206 records, 40 km²), Virgin Gorda (17 SCC, 665 records, 22 km²). All other islands had ten or fewer
Figure 1. Map of TIPAs and terrestrial National Parks of the British Virgin Islands. Detailed maps at the bottom showing overlap of TIPAs and National Parks in those Islands. Abbreviations: Tropical Important Plant Areas (TIPAs), National Park (NP), Proposed National Park (Proposed NP).
Table 1. Species of Conservation Concern, their threat status, distribution and occurrence in TIPAs and National Parks. All species names according to Plants of the World Online Portal (POWO 2021). Globally threatened status according to IUCN criteria v. 13. IUCN assessments under synonyms for four species †Bastardiopsis eggersii (Baker f.) Fuertes & Fryxell, ‡Calyptranthes kiaerskovii Krug & Urb., §Calyptranthes thomasiana O.Berg and ∥Acacia anegadensis Britton. Abbreviations: Neotropics (NTROP), Caribbean Region (CARIB), Puerto Rican Bank Floristic Region (PRB), US and British Virgin Islands (VI), British Virgin Islands (BVI) and Puerto Rico (PR), Tropical Important Plant Areas (TIPAs), National Park (NP), Proposed National Park (PNP).

| Species                  | Family              | IUCN assessment | Endemism | Total records | TIPAs present | NP present | PNP present |
|--------------------------|---------------------|-----------------|----------|---------------|---------------|------------|-------------|
| Agave missionum Trel.    | Asparagaceae        | VU              | PRB      | 220           | 11            | 4          | 2           |
| Anthurium × selloanum K.Koch | Araceae            | N/A            | VI       | 11            | 2             |            |             |
| Argythamnia stahlisi Urb. | Euphorbiaceae      | VU              | PRB      | 104           | 2             | 1          |             |
| Abutilon virginianum Krapov. | Malvaceae        | EN              | PRB      | 67            | 4             | 1          |             |
| Myrcia neokiaerskovii E.Lucas & K.Samra | Myrtaceae | CR              | BVI, PR  | 32            | 2             | 2          |             |
| Myrcia neothomasiana A.R.Loureño & E.Lucas | Myrtaceae | EN              | VI       | 23            | 2             | 2          |             |
| Cedrela odorata L.       | Meliaceae          | VU              | NTROP    | 1             | 1             | 1          |             |
| Croton falsiocris Britton | Euphorbiaceae      | NT              | VI       | 295           | 8             | 2          | 1           |
| Erythrina eggersii Krukoff & Moldenke | Leguminosae | EN              | PRB      | 11            | 2             | 1          |             |
| Galactia eggersii Urb.   | Leguminosae        | EN              | NT       | 34            | 5             | 1          |             |
| Guaicaceum officinale L. | Zygophyllaceae     | EN              | NTROP    | 15            | 1             | 1          |             |
| Ilex urbaniana Loes. ex Urb. | Aquifoliaceae | PRB             | VI       | 21            | 1             | 1          |             |
| Leptocereus quadricostatus (Bello) Britton & Rose | Cactaceae | EN              | BVI, PR  | 33            | 1             | 1          |             |
| Machaonia woodburyana Acex.-Rodr. | Rubiaceae | EN              | VI       | 141           | 2             |            |             |
| Malpighia woodburyana Vivaldi | Malpighiaceae     | VU              | PRB      | 262           | 12            | 3          | 4           |
| Maytenus cymosa Krug & Urb. | Celastraceae       | EN              | PRB      | 35            | 2             | 1          |             |
| Metastelma anegadensis Britton | Apocynaceae      | EN              | BVI      | 212           | 2             | 1          |             |
| Micinia thomasiana DC.   | Melastomataceae    | NT              | BVI, PR  | 24            | 1             | 1          |             |
| Mitracarpus polyalud. Urb. | Rubiaceae          | EN              | CARIB    | 36            | 1             |            |             |
| Peperomia wheeleri Britton | Piperaceae         | EN              | CARIB    | 7             | 2             |            |             |
| Picrama excelsa (Sw.) Planch. | Simaroubaceae | VU              | NTROP    | 1             | 1             | 1          |             |
| Pilea sanctae-cruis Liebm. | Urteaceae          | EN              | VI       | 16            | 3             | 2          |             |
| Piptocoma antillana Urb. | Asteraceae         | LC              | PRB      | 14            | 4             | 1          |             |
| Pitcairnia jarecki Proctor & Cedeño-Mald. | Bromeliaceae | EN              | BVI      | 17            | 3             |            |             |
| Psychilis macconvillei Sauleda | Orchidaceae     | NT              | BVI      | 35            | 9             | 1          | 2           |
| Reynosia guama Urb.      | Rhamnaceae         | NT              | VI       | 32            | 6             | 2          |             |
| Rondeletia pilosa Sw.    | Rubiaceae          | NT              | PRB      | 60            | 9             | 2          | 2           |
| Sabal catenatum (O.F.Cook) Becc. | Arecaaceae  | VU              | CARIB    | 26            | 3             | 1          |             |
| Senna polyphylla var. neglecta H.S.Irwin & Barney | Leguminosae | CR              | BVI      | 78            | 1             | 1          |             |
| Tillaenda × linearispatha Mex | Bromeliaceae     | N/A             | PRB      | 9             | 3             | 2          |             |
| Tolumnia priocola (Kraenzl) Bream | Orchidaceae | NT              | BVI      | 31            | 6             | 1          | 1           |
| Vachellia anegadensis (Britton) Seigler & Ebinger | Leguminosae | EN              | BVI      | 705           | 1             | 1          | 1           |
| Varronia ripicola (Urb.) Britton | Boraginaceae | EN              | BVI, PR  | 923           | 1             | 1          |             |
| Zanthoxylum flavum Vahl   | Rutaceae           | VU              | NTROP    | 18            | 1             | 1          |             |
| Zanthoxylum thomasianum Krug & Urb. | Rutaceae          | EN              | PRB      | 139           | 2             | 1          |             |

SCC and < 75 records, including Jost Van Dyke which is the fourth largest island in the archipelago (8 km²). Regional endemism was high, with 13 species endemic to the Puerto Rican Bank, seven to the Virgin Islands (BVI and USVI), four to the BVI only and four occurring in the BVI and Puerto Rico, but absent from the USVI. Species with a Neotropical or wider Caribbean distribution were also included in the SCC list (Table 1) because they are globally threatened and qualified for TIPAs.
Species richness across the BVI archipelago. Data show number of Species of Conservation Concern (SCC) recorded in each island. Numbers in () correspond to globally threatened species.

The three largest islands contained higher species richness and number of records (Fig. 2), i.e. Tortola (14 globally threatened species, 132 records), Anegada (nine globally threatened species, 2192 records) and Virgin Gorda (12 globally threatened species, 390 records).

Species richness within TIPAs

The BVI TIPAs network contains 18 sites distributed across the archipelago (Fig. 1). Individual TIPAs sites varied in size from entire islands to small areas within islands, the largest being Anegada Island TIPA with 38 km² and the smallest Hawks Nest with 0.37 km². The qualifying criteria for TIPAs do not take into consideration land ownership and highly-disturbed urban areas were excluded from TIPAs boundaries.

All Species of Conservation Concern are represented across the BVI TIPAs Network with ca. 91% of all records occurring within TIPAs (Fig. 3). The only TIPA that does not have any of the SCC present is Paraquita Bay and Bar Bay TIPA which is based solely on a threatened habitat (Mangroves). The greatest number of records (Table 2) were available for Anegada Island TIPA (2206 records), followed by Central...
### Table 2. TIPAs Network and occurrence of Species of Conservation Concern in the British Virgin Islands. Location of TIPA in () if not contained in the TIPA name. Abbreviations: Tropical Important Plant Area site (TIPA).

| Species of Conservation Concern | Anguilla Island TIPA | Bed Island and the Channel TIPA | Carriacou and the Channel TIPA | Eastern Scrub Island TIPA | Ginger Island TIPA | Great Tobago Island TIPA | Guana Island TIPA | Hawks Neck TIPA (Tortola) | Mount Sage TIPA (Tortola) | Norman Island TIPA | Northern Great Camanoe TIPA | Northern Great Camanoe TIPA | NORTHERN EASTERN TIPASA | Prickly Pear Island TIPA | Prickly Pear Island TIPA | Prickly Pear Island TIPA | Total records within TIPAs |
|---------------------------------|---------------------|-------------------------------|-------------------------------|----------------------------|-------------------|------------------------|----------------|------------------------|------------------------|----------------|-------------------------|-------------------------|--------------------------|------------------------|------------------------|------------------------|--------------------------|
| **Species**                     |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        |                      |
| Agave missionum                | 73                  | 9                             | 8                             | 33                         |                   | 20                     | 15             | 3                      | 15                     | 10            |                        |                        | 1                       |                        | 1                      | 2                      | 204                     |
| Anthurium × selloanum          |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        |                      |
| Argyranthemum stahlii          |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        |                      |
| Abutilon virginianum           | 102                 |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 103                     |
| Myrcia neothomasiana           | 14                  |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 32                      |
| Cedrela odorata                 |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 23                      |
| Croton fuscifoli                |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 259                     |
| Erythrina eggersii             |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 11                      |
| Galactia eggersii              |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 30                      |
| Guaiacum officinale            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 15                      |
| Ilex urbaniana                 |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 21                      |
| Leptocereus quadricostatus     |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 33                      |
| Machaerina woodburyana         |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 116                     |
| Malpigia woodburyana           |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 174                     |
| Maytenus cymosa                |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 33                      |
| Metallotus anagadense           |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 212                     |
| Miconia thomasiana             |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 24                      |
| Mitracarpus polyedrus           |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 36                      |
| Peperomia wheeleri             |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 7                       |
| Plectranthus excelsa            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 1                       |
| Pilea sanctae-cruis            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 13                      |
| Piptocoma antillana            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 10                      |
| Pittatrinia jarettii            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 17                      |
| Psychotria macconelliae         |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 34                      |
| Reynosia guama                 |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 30                      |
| Rondeletia pilosa              |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 45                      |
| Sabal causiarum                |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 18                      |
| Senna polypylla var. neglecta  |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 18                      |
| Tillandisia × linearisepica    |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 8                       |
| Tolomia prionochila            |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 26                      |
| Vachellia anagadensis           |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 644                     |
| Varronia rupeola               |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 923                     |
| Zanthoxylum flavum             |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 18                      |
| Zanthoxylum thomasianum        |                     |                               |                               |                            |                   |                        |                |                        |                        |                |                        |                        |                         |                        |                        |                        | 123                     |
| **Total records**              | 2206                | 72                            | 469                           | 47                      | 103               | 14                    | 42              | 28                     | 74                      | 104             | 75                       | 55                       | 5                        | 13                    | 0                      | 30                     | 10                    | 8                      | 3353                     |
| **Number of species**          | 14                  | 8                             | 17                            | 6                       | 8                 | 2                      | 6               | 4                      | 10                     | 12              | 9                        | 4                        | 1                       | 3                      | 0                      | 5                     | 5                      | 3                       | 35                      |
| **Globally threatened species**| 12                  | 2                             | 9                             | 2                       | 3                 | 3                      | 2               | 6                      | 6                       | 6               | 3                        | 1                       | 3                      | 2                      | 0                      | 2                     | 1                      | 2                       | 25                      |
Virgin Gorda TIPA (469 records) and Hawks Nest TIPA (104 records). These TIPAs also had high species richness and several globally threatened species (Fig. 4). Interestingly, Hawks Nest TIPA on Tortola has a high SCC concentration in a small area (0.37 km²) when compared to the largest sites on Virgin Gorda: Central Virgin Gorda TIPA and Eastern Virgin Gorda TIPA with 7.8 km² and 2.7 km², respectively.

All BVI globally threatened species are present in the BVI TIPAs Network (Table 1). Nine species have more than half of their records within TIPAs and 15 species have all their records within TIPAs, including three BVI endemic species. The other BVI endemic, *Vachellia anegadensis*, also occurs on the Island of Fallen Jerusalem which did not qualify as a TIPA, but is a National Park. The only two globally threatened species poorly represented in the TIPAs Network were *Abutilon virginianum* Krapov. (43.3%) and the natural hybrid *Anthurium × selloanum* K.Koch (18.2%) (Fig. 3). The two most widespread globally threatened species were *Agave missionum* Trel. and *Malpighia woodburyana* Vivaldi occurring in 11 and 12 of the TIPAs, respectively. The two rarest globally threatened species are the Neotropically-distributed *Cedrela odorata* L. and *Picrasma excelsa* (Sw.) Planch. with only one high accuracy record each on the Island of Tortola, both in Mount Sage TIPA and Sage Mountain National Park (Tables 2 and 3).

The Central Virgin Gorda TIPA is the site with the highest species richness with 17 Species of Conservation Concern (Fig. 4). None of these species is exclusive to this site.
Figure 4. Species richness within the BVI TIPAs network. Data show number of Species of Conservation Concern, comprised of globally threatened species and restricted range species which are not globally threatened, in each TIPA site.

Two Puerto Rican Bank endemic species, *Myrcia neokiaerskovii* E.Lucas & K.Samra and *Myrcia neothomasiana* A.R.Lourenço & E.Lucas, are only found in the threatened Upland Evergreen Forest habitat within this TIPA and Mount Sage TIPA (Table 2). These species have, respectively, ca. 97% and 87% of their records within Gorda Peak National Park and Sage Mountain National Park (Table 3). Even though these two TIPAs share the same habitat type and some common species, there are important and rare plants that occur in one, but not the other. The Eastern Virgin Gorda TIPA has no exclusive species and lower species richness than the Central Virgin Gorda TIPA, but this site contains > 1% of the global population of the Puerto Rican Bank endemic *Maytenus cymosa* Krug & Urb. and > 5% of the national population of the Virgin Islands endemic *Machaonia woodburyana* Acev.-Rodr. Central Virgin Gorda TIPA is also one of the five best sites in the BVI for two nationally threatened habitats: Coastal Shrubland and Mangroves.

Half of the globally threatened species found in the Anegada Island TIPA are not present on any other island in the BVI (Table 2). This includes *Varronia rupicola* and *Leptocereus quadricostatus* (Bello) Britton & Rose, found on Anegada and Puerto Rico and the BVI endemic *Senna polyphylla* var. *neglecta*. This TIPA has the second highest species richness in the BVI with 14 Species of Conservation Concern (Fig. 4). The Island of Anegada currently lacks designated terrestrial protected areas. The only high accuracy records for *Guaiacum officinale* L. are from this Island, but the species is also reported from Guana, Jost Van Dyke, Tortola and Virgin Gorda (The BVI TIPAs National Team 2019b, 2019a). Guana Island TIPA is a species-rich site with 10 Species of Conservation Concern and almost all records for the BVI endemic *Pitcairnia jareckii*. 
Table 3. National Parks and occurrence of Species of Conservation Concern in the British Virgin Islands. National Parks without any records for the species are not listed. Location of National Park in () if not entire island. † Indicates percentage instead of number of records.

| Species of Conservation Concern | Existing National Parks (NP) | Proposed National Parks (PNP) |
|---------------------------------|-----------------------------|--------------------------------|
|                                  | Cam Bay (Great Camanoe)     | Dead Chest Island              |
|                                  | Fallen Jerusalem            |                            |
|                                  | Great Thatch                |                            |
|                                  | Prickly Pear                |                            |
|                                  | Sage Mountain (Tortola)     |                            |
|                                  | Shark Bay (Tortola)         |                            |
|                                  | Spring Bay (Virgin Gorda)   |                            |
|                                  | Total records within NP     | Occurrence within NP (%)     |
| Agave missionum                  | 2                           | 24                            |
| Anthurium × selloanum            | 20                          | 11                            |
| Argythamnia stapilli             | 1                           | 8                             |
| Abutilon virginianum             | 17                          | 4                             |
| Myrcia neothomasiana             | 11                          | 14                            |
| Cedrela odorata                  | 1                           | 100                           |
| Croton fishlockii                | 13                          | 17                            |
| Erythrina eggersii               | 1                           | 4                             |
| Guaiacum officinale              | 10                          | 23                            |
| Ilex urbaniana                   | 21                          | 8                             |
| Leptocereus quadricostatus       | 1                           | 1                              |
| Machaonia woodburyana            | 1                           | 10                            |
| Malpighia woodburyana            | 2                           | 16                            |
| Maytenus cymosa                  | 8                           | 6                             |
| Metastelma anegadenie            | 8                           | 1                             |
| Miconia thomasiana               | 13                          | 13                            |
| Mirracarpus polygaladus          | 2                           | 12                            |
| Peperomia wheelei                | 1                           | 1                             |
| Picrasma excelsa                 | 3                           | 4                             |
| Pilea sauciae-cruici             | 4                           | 4                             |
| Piptocoma antillana              | 4                           | 2                             |
| Psychilis micconelliace          | 4                           | 4                             |
| Reynosia guama                   | 4                           | 11                            |
| Rondoletia piloosa               | 3                           | 5                             |
| Sabal causiarum                  | 3                           | 3                             |
| Senoa polyphylla var. neglecta   | 2                           | 2                             |
| Tillandisia × lineatissima       | 1                           | 2                             |
| Toluwnia prionochila             | 9                           | 29                            |
| Vachellia anagadenis             | 61                          | 61                            |
| Varroaria rapicola               | 36                          | 36                            |
| Zanthoxylum flavum               | 4                           | 4                             |
| Zanthoxylum thomasianum          | 21                          | 21                            |
| **Total records**                | 272                         | 74†                            |
| **Number of species**            | 272                         | 74†                            |
| **Globally threatened species**  | 252                         | 215                           |

The two sites with lowest species richness, Paraquita Bay and Bar Bay TIPA on the Island of Tortola and Northeastern Jost van Dyke TIPA (Fig. 4), both qualified as a TIPA for their importance for threatened habitats, the former for its Mangroves and the latter for its Semi-deciduous Gallery Forest.
Ginger Island TIPA is also low in species richness but qualified for being one of the five best sites in the archipelago for the globally threatened *Abutilon virginianum*. This species is also present in Guana Island TIPA, Norman Island TIPA and Sabbath Hill TIPA on the Island of Tortola. Only three records for this species are within a protected area in Dead Chest National Park (Table 3) and 43% of the records are found within TIPAs (Fig. 3).

**Species richness within BVI National Parks**

A small proportion of all observed records were recorded in National Parks (ca. 7%) and Proposed National Parks (5.3%), occurring in only 10 of the 21 National Parks and four of the eight Proposed National Parks. In terms of species, two thirds of the Species of Conservation Concern (22 species), including nearly half of the globally threatened species (13 species), are represented in the BVI National Park System, having legal protection (Table 3). If we include Proposed National Parks to the analysis, then the number of Species of Conservation Concern increases to 31 species. However, only six of these species have > 50% of their records within National Parks. The species that had all records within National Parks were *Cedrela odorata*, *Picrasma excelsa* and *Ilex urbaniana* Loes. ex Urb., all occurring in Sage Mountain National Park on the Island of Tortola.

Five of the Species of Conservation Concern, i.e. *Argythamnia stabilis* Urb., *Guaiacum officinale*, *Senna polyphylla* var. *neglecta*, *Varronia rupicola* and *Zanthoxylum flavum* Vahl, were absent from National Parks, but occurred in the Eastern Ponds Proposed National Park on the Island of Anegada. Similarly, *Erythrina eggersii* Krukoff & Moldenke and *Galactia eggersii* Urb. are only present in the Great Thatch Proposed National Park on the Island of Great Thatch. Gorda Peak National Park on the Island of Virgin Gorda and Sage Mountain National Park on the Island of Tortola have the highest observed number of Species of Conservation Concern (eight for each), including, respectively, four and six globally threatened species. The species absent from the National Parks System were *Machaonia woodburyana*, *Mitracarpus polycladus* Urb. and *Pitcairnia jareckii*. Despite *Peperomia wheeleri* Britton occurring in Gorda Peak National Park, a lack of high-resolution records resulted in the species not being recorded in our dataset (Table 3).

Overlaps between TIPAs sites and six of the National Parks are observed on the Islands of Tortola, Virgin Gorda, Prickly Pear and Great Camanoe (Fig. 1). Another three Proposed National Parks overlapped with TIPAs on Beef Island, Great Thatch and Anegada.

**Discussion**

**Data and species distribution**

Records from non-georeferenced sources or those georeferenced, but without the required high accuracy (+/- 10 m), were not considered in the analysis, thus improving
standardisation and increasing confidence in the results. Herbarium vouchers and/or photographs accompanied most records. Field surveys conducted by those familiar with the species and trained botanists ensured correct plant identifications. As not all islands of the BVI archipelago could be surveyed in the given project timeframe (2016–2019), gap analysis and consultation with partners ensured the dataset had a representative coverage across the archipelago. Measures applied to avoid data duplication included the use of high accuracy data in the analysis, filtering and checking records before retrieval from the main database, gap analysis, planned fieldwork targeting new areas and use of handheld computers with GPS during fieldwork to visualise previously-recorded observations. Combining all data from herbarium vouchers and field observations into one dataset and incorporating them into the GIS also enabled us to check and visualise data for any possible errors and duplications. The dataset used for the identification of TIPAs and analysed here is for the 35 Species of Conservation Concern occurring across 23 of the BVI islands, so it does not represent the complete botanical richness of each island, TIPA or National Park. Having an initial target list of priority species with all the known regional (Puerto Rican Bank) and national endemic native plant species enabled focused field surveys and a robust dataset for assessing the current threats and extinction risk for these species.

There was large variation in the numbers of records for each species (1–923) and per island (1–2206) because of the various sources of data used in this analysis, sampling effort and site botanical richness. Anegada Island, in particular, had a large amount of data available (2206 records) due to previous, focused research on *Vachellia anegadensis* (Bárrios 2015; Bárrios et al. 2021), *Varronia rupicola* (Hamilton 2016) and other threatened species, such as *Argythamnia stahlii* and *Metastelma anegadense* (Linsky 2014). This explains the high number of records for this Island and these species in this analysis. Several other species have also been the focus of survey and sampling efforts, particularly national and regional endemics.

The number of Species of Conservation Concern and globally threatened species per island did not relate directly to land area, as we observed that some small islands have greater species richness for these categories than larger islands, for example, Guana and Jost van Dyke (Fig. 2). Besides possible sampling bias, other factors, such as history of management and habitat intactness because of urban development, invasive species and feral grazing, are more likely to affect species composition than size alone. Guana Island has been privately owned since 1935 and is mostly undeveloped with feral grazing animals removed in the past (goats) or being controlled (sheep) (Mayer and Chipley 1992; Island Resources Foundation 2015a). On the other hand, Jost van Dyke is more developed with a higher level of disturbance from feral grazing and invasive alien species (Island Resources Foundation and Jost Van Dykes (BVI) Preservation Society 2009), both of which have negative impacts on native plant species persistence and discovery during surveys.

### Species richness and conservation within TIPAs and National Parks

More than 66% of the Tropical Dry Forests of the Caribbean are estimated to have already been lost and native species richness and population numbers reduced (IPBES...
2018). Botanical data, such as those presented here, are urgently needed to guide efforts to limit further biodiversity loss. The aim of the TIPAs framework is to identify a network of areas that represent the most important sites for the conservation and management of species of global and or local conservation concern for a specific region or country/territory (Darbyshire et al. 2017). This target was achieved through the identification of the BVI TIPAs Network, as its sites are well distributed across the archipelago (Fig. 1) and all Species of Conservation Concern are represented. All globally threatened species, apart from Abutilon virginianum, have > 50% of their high-resolution records within TIPAs and 15 species have all available high-resolution records within TIPAs. The TIPAs criterion A(i) aims to capture areas that contain > 1% of the global population or > 5% of the national population of a globally threatened species (Darbyshire et al. 2017), resulting in a good representation of species across the TIPAs Network. The four BVI endemic species are well represented within TIPAs, but that is not the case within the current BVI Protected Areas System Plan 2007–2017. Vachellia anegadensis is the only BVI endemic plant species present in a Protected Area as it occurs within the Fallen Jerusalem National Park. However, most of its population (> 90%) is found on the Island of Anegada, which currently has no designated terrestrial protected areas.

Data showed that the Island of Anegada has the highest number of Species of Conservation Concern in the BVI. The Anegada Biodiversity Action Plan (2003–2006) (McGowan et al. 2006) identified 288 native plant species for the Island with 4% of them being endemic to the Puerto Rican Bank Floristic Region. This species richness and endemism can be partially explained by the Island’s geological history, which is unique for the BVI. While all the other islands in the BVI are of volcanic origin, Anegada is formed completely of limestone (Gore 2013). Another factor is that the Island is mostly undeveloped. The major threat for most plant species on the Island is grazing by feral animals with numerous cows, sheep, goats and donkeys roaming free; however, invasive insect pests are an increasing threat to the flora (Malumphy et al. 2015; The BVI TIPAs National Team 2019b). McGowan et al. (2006) suggested the establishment of a protected area network to protect key habitats and species on the Island and land zoning to protect critical habitats across the Island. Two areas were proposed in the BVI Protected Areas System Plan (2007–2017) for this Island, the Eastern Ponds Proposed National Park and the Western Ponds Protected Landscape, both already identified as RAMSAR sites (Gardner et al. 2008). The addition of these two areas to the BVI protected area network would increase the number of species under protection, although the largest part of the populations would remain outside these areas and under potential threat. The identification of the whole Island as a TIPA site indicates the importance of considering a wider approach, such as inclusion of additional areas during any future revision of the BVI Protected Areas System Plan or private nature reserves.

The current BVI National Parks System does not hold a good representation of the Species of Conservation Concern, with species completely absent or only a small number of individuals present (Table 3). It has been shown that protected ar-
BVI TIPAs, plant species richness and conservation

Eas globally fall short on having a representative coverage of biodiversity and future expansions should take that into account for effective conservation (Butchart et al. 2015). The small number of SCC individuals present in the current BVI National Parks System undoubtedly means the system does not capture the full genetic diversity of most of the species. Studies have shown that fragmentation, reduction in population size and loss of genetic diversity can affect species fitness and survival rates (Reed and Frankham 2003; Frankham 2005). This is cause for concern due to the increasing pressures these species face because of urban development, habitat fragmentation, feral grazing, encroachment of invasive species and climate change. More than 40 invasive insect pests were observed in the BVI during a rapid survey by Malumphy (2017) and > 260 species of invasive plants have been recorded so far with 18 of them flagged as the most serious (The BVI TIPAs National Team 2019b). Invasive species are a regional and global problem which drives population declines and species extinctions and can lead to major socio-economic impacts (Kairo et al. 2003; Reaser et al. 2007; Vilà et al. 2011).

Two National Parks, Great Tobago and Prickly Pear, which qualified as TIPAs for their botanical richness and occurrence of Species of Conservation Concern, are under extreme environmental pressure despite legal protection. Both areas have been heavily grazed by feral animals and invasive species are displacing native vegetation (The BVI TIPAs National Team 2019b). This highlights that alongside legal protection, resources for management and enforcement are a necessary long-term commitment. Protocols for invasive plant species eradication and long-term monitoring of the vegetation recovery after feral animal eradication have been established and require long-term resourcing (Hamilton et al. 2019).

Global evidence suggests that inaccessible areas, such as steep cliffs and ghuts, exhibit higher species richness and are home to several rare species (Norder et al. 2020). This is the case of Hawks Nest TIPA on Tortola. Most of the area, mixed Crown and private land, is undeveloped due to its steep and rugged hillsides which prevented earlier settlements and plantations. Development of the land within this TIPA could lead to clearing of the vegetation and possible loss of genetic diversity and reduction of population numbers for several important species. Two Puerto Rican Bank endemic species, Erythrina eggersii and Zanthoxylum thomasianum Krug & Urb. and the Virgin Islands endemic Pilea sanctae-cruccis Liebm. could be particularly affected as they only occur in a few locations in the BVI. Research is needed to evaluate the importance of the various sites containing individuals for the conservation of their genetic variability. Land swaps could provide an option for retaining unique habitat in the BVI.

Sage Mountain National Park on Tortola and Gorda Peak National Park on Virgin Gorda are, respectively, within Mount Sage TIPA and Central Virgin Gorda TIPA. These sites have a high number of Species of Conservation Concern. Settlements on both Islands date to Pre-Colombian times and European colonisation in the 17th century led to large-scale deforestation for plantations and urbanisation in the following century. Presently, these Islands are home to most of the BVI hu-
man population, Tortola 83% and Virgin Gorda 14% (Island Resources Foundation 2012, 2015b). The early recognition by the BVI Government of these areas as important sites for soil and watershed management, conservation of Caribbean forests and tourism and recreation led to their designation as National Parks as early as 1964 for Sage Mountain (Forestry Area since 1955) and 1974 for Gorda Peak (Gardner et al. 2008). This ensured a level of protection of the local flora and rare Upland Evergreen Forest threatened habitat, which only occurs in these two areas of the BVI due to their higher altitudes (up to 526 m) and moister environment (The BVI TIPAs National Team 2019b). Besides legal protection, several taxa require species management plans to monitor threats and create ex situ collections to ensure future survival. For example, Myrcia neokiaerskovii and Myrcia neothomasi ana are only found in these two National Parks in the BVI. Both have a small number of individuals and are currently threatened by several invasive scale insects (Malumphy et al. 2019) and the impacts of climate change, making them susceptible to extinction. The fragility of small populations, regardless of their location in relation to National Park boundaries, highlights the need for on-going monitoring and securing these species in ex situ collections (Hamilton et al. 2017; Clubbe et al. 2020). Genetic diversity and representation in ex situ collections are important to prevent genetic erosion and inbreeding, maximise the potential for future re-introductions and species management interventions (Lauterbach et al. 2012; Hoban and Strand 2015; Wood et al. 2020). Regional collaborations are also important for understanding species genetic diversity across borders and implementing species management plans.

Pathway to future plant conservation in the BVI and Caribbean

Surveys of Caribbean conservation organisations revealed an existing knowing-doing gap for more effective local conservation (Jacobs et al. 2016). The BVI TIPAs process was able to bridge the gap between practitioners and scientists by including both groups, not only in decision-making, but also data gathering and sharing. Robust georeferenced data for Species of Conservation Concern, globally threatened species and threatened habitats of the BVI have been made available through this process for in situ and ex situ plant conservation, enabling targeted and more focused species management, recommendations during revision of physical planning applications and development of environmental policy. Hawks Nest TIPA on Tortola is a good example of an area previously not well documented and where a high number of Species of Conservation Concern were recorded through field surveys during the TIPAs process. These new data highlighted the area as a priority for monitoring and management of several globally threatened species, including Zanthoxylum thomasi anum. Since then, further surveys of Z. thomasi anum in the area increased the number of known individuals and contributed samples for genetic studies. This species is now being monitored regularly on Tortola and Virgin Gorda. Ex situ conservation via seed collections and propagation at J.R. O’Neal Botanic Gardens on Tortola is underway. Furthermore, threatened
species data for Hawks Nest TIPA have been crucial and timely to make informed decisions on recent planning applications to develop part of the area.

The role of the BVI National Parks as an education resource to engage the local communities (Smith-Abbott et al. 2002) have been applied to the BVI TIPAs through workshops, field guides and interpretation panels delivered via the TIPAs process (The BVI TIPAs National Team 2019a, 2019b). Research has shown that the local communities tend to a passive attitude towards conserving biodiversity in protected areas, but that can be changed by engagement and livelihood projects (Watson et al. 2014; Tumbaga et al. 2021). In the future, boundary organisations can be engaged to maximise awareness and participation in plant conservation efforts in the BVI via such initiatives.

Ideally, the integration of the TIPAs network into a revised BVI Protected Areas System Plan under National Parks or other management categories would be highly beneficial for the future conservation of the Species of Conservation Concern and threatened habitats in the BVI, helping minimise biodiversity loss and improving species management and monitoring of threats, such as invasive species. However, this approach is neither practical nor feasible as some TIPAs sites are entire islands and or private property. A focused assessment on what areas within the TIPAs network should be declared as protected areas is required to ensure a certain percentage of the Species of Conservation Concern and the threatened habitats identified are protected. In the Republic of Guinea, researchers are working with the local government to integrate some of the TIPAs into the protected areas system, safeguarding and benefitting, not only local flora, but also fauna as the areas are under severe threat (Couch et al. 2019b).

Intact habitats show resilience to natural disasters, as observed in the BVI after the category 5 Hurricane Irma ravaged the islands in 2017 (Hamilton and Clubbe 2018). Caribbean Dry Forests have evolved to withstand and recover after hurricane events (Van Bloem et al. 2006). Such resilience has significant impacts, not only in the maintenance of species diversity and ecosystem services (e.g. reducing soil erosion, food for fauna), but also indirect socio-economic benefits, such as ecotourism.

Despite the benefits of in situ conservation, there are limitations in terms of resources required, land ownership and local interests. Locations of global protected areas show a bias towards higher elevations, steeper slopes, lands of lower productivity and economic worth and low human density and are often not representative of local biodiversity. Expansions driven by Aichi Target 11 can only change this scenario if threatened species distributions are considered and trade-offs of costs and benefits properly managed (Watson et al. 2014). As discussed previously, legal protection alone is not enough to ensure species survival, as many of the Species of Conservation Concern are found outside the Protected Areas System or are under threat by feral grazing and/or invasive species. The TIPAs process in the BVI delivered spatial data and extinction risk assessments for the Species of Conservation Concern and threatened habitats, which can be used to help provide information for development planning during the Environmental Impact Assessment process, minimising further biodiversity loss. A combined plan of in situ and ex situ conservation is the best approach to maximise resources and prevent loss of genetic diversity and species extinctions. Ex situ col-
lections for threatened and/or endemic species of the BVI and the Puerto Rican Bank Floristic Region have been developed over recent years (Gdaniec and Hamilton 2017; Hamilton et al. 2017), but much needs to be done to fully evaluate the impact of such collections on species conservation and reduction of biodiversity loss.

Knowledge of the status and distribution of botanical resources is important for good conservation decision-making and to meet international targets set in Multi-Lateral Environmental Agreements (CBD 2011; GSPC 2021). Clubbe, Hamilton and Corcoran (2010) identified the GSPC as an important document for plant conservation in the UKOTs and much has been achieved so far towards delivering Targets 1 (check-list) and 2 (Red List) for each Territory (Clubbe et al. 2020). TIPAs form the basis of Target 5 of the GSPC and also align with Key Biodiversity Areas (KBAs), which are sites contributing significantly to the global persistence of biodiversity (IUCN 2016). The identification of TIPAs, using comprehensive scientific data specific to the BVI, has identified gaps in the existing BVI Protected Areas System Plan and will contribute to an updated version of the System Plan using the criteria for protected area designation. Further survey work could identify core areas of plant species abundance and diversity which would help to refine TIPAs boundaries, particularly where whole islands are currently identified as TIPAs. Combining these detailed plant data with genetic data available for threatened species, vegetation maps and data on other key taxa, such as birds, amphibians, reptiles and invertebrates can further refine site selection for new protected areas. The identification of TIPAs within the BVI can also provide information for the creation of Environmental Protection Areas (EPAs) under the Physical Planning Act (Government of the Virgin Islands 2004). Development would be strictly controlled in these areas and would have to comply with permitted use activities. This would assist the BVI in meeting the Sustainable Development Goals target 15.5, which aims to reduce the degradation of natural habitats, halt the loss of biodiversity and protect and prevent the extinction of threatened species (United Nations 2021).

All available botanical data for native and invasive species in the BVI generated through this work have been shared with BVI partners to be integrated into the National Geographic Information System (GIS) and is curated through the Kew UKOTs SSD (UKOTsTeam 2021). A complete analysis of all botanical data available for the BVI could reveal biogeographical patterns, provide information for extinction risk assessments, biodiversity conservation and species management in the future and should be considered a priority.

**Conclusion**

The TIPAs model developed for the BVI, the first of its kind in the Caribbean, has been successful in identifying and mapping plant species of national and global conservation concern and areas important for plant conservation in the BVI. The robust and extensive botanical dataset generated was used to deliver native species identification and distribution, provide information for extinction risk assessments and the identi-
The integration of this resource into the National GIS of the BVI and access by local practitioners and policy-makers can help guide and focus future conservation efforts and resources, facilitating species management and recovery efforts. This model has wider applications across the Caribbean, particularly to other UK Overseas Territories. Discussions held at the international TIPAs workshop in April 2019 on Tortola, BVI, highlighted the potential and benefits that the identification of TIPAs can have to deliver robust data for conservation management and action across the Caribbean Region (The BVI TIPAs National Team 2019a).

Data analysed here have highlighted the importance of the BVI National Parks System for plant and ecosystem conservation. However, the BVI TIPAs network has identified areas outside of the existing Protected Area Network that require protection measures to be put in place to conserve globally threatened plant species and habitats. Data on the Species of Conservation Concern and the TIPAs network will be important in addressing gaps and providing information for the current revision of the BVI Protected Areas System Plan and physical planning applications.

Acknowledgements

We thank HSBC for funding the project ‘Tropical Important Plant Areas of the British Virgin Islands’ through their 150th fund and the Kew Foundation for assisting in accessing these funds. Thanks to regional partners, Jeanine Gavilan-Velez (University of Puerto Rico, MAPR Herbarium), Omar Monsegur (USFWS CESFO) and José Sustache (DRNA) for their participation in fieldwork, TIPAs and Red List assessments workshops in the BVI and openly sharing their knowledge and experiences to assist species threat assessments and field survey. Thanks to Alex Roberts and Rosemary Foley (Kew) for their assistance compiling information for the IUCN Red List assessments and digitising herbarium specimens. Thanks to Lynda Varlack and Tessa Smith for their participation in the BVI TIPAs National Team and their contribution to the identification of the BVI TIPAs Network.

Declarations

This research was funded by the HSBC 150th Anniversary Fund. The authors declare that they have no conflict of interest. Data were obtained with approval of the Virgin Islands Government via the National Parks Trust of the Virgin Islands.

Credits

All authors whose names appear on the submission: 1) made substantial contributions to the conception or design of the work; or the acquisition, analysis or interpretation of data; 2) drafted the work or revised it critically for important intellectual content; 3) approved the version to be published; and 4) agree to be accountable for all aspects of
the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. The full datasets generated during and/or analysed during the current study are not publicly available due to the need to protect precise locations of threatened species, but are available from the corresponding authors on reasonable request. Vetted data for the BVI TIPAs Network are publicly available via the Kew Tropical Important Plant Areas Explorer (https://tipas.kew.org).

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Waterbird assemblages of inland wetlands in Chile: A meta-analysis

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Abstract

Chile has a large number of wetlands that offer a wide variety of refuges and food to waterbird assemblages. This research hypothesises that these assemblages differ according to the structural characteristics of each type of inland wetland. The object is to identify the structure of these assemblages, evaluating their richness, alpha α diversity and some ecological characteristics, taxonomic structures and trophic guilds. We performed a meta-analysis by submitting pre-selected articles to multivariate reliability analysis. The selected articles were used to characterise the assemblages by alpha α diversity: species richness, Shannon-Wiener index, Pielou’s Evenness Index, relative abundance and taxonomic distinctiveness Δ + and beta β diversity: Bray-Curtis with analysis of similarity percentage. Diversity and evenness differed in the seven wetlands studied, among 12 to 45 species, Shannon-Wiener index H’= 0.08 to 0.94 bits and Pielou’s Evenness Index J= 0.06 to 0.71. Four wetlands were below and three above the expected value for taxonomic distinctiveness (Δ +) (73.2 units). Two clusters were identified using the β diversity: one consisting of the High-Andean wetlands (Huasco and Negro Francisco); and the other of El Peral lagoon, the Cruces River wetlands complex and the Tráns Traf San Rafael man-made wetland. The most remarkable dissimilarity was provided by three species (Cygnus melancoryphus, Phoenicoparrus jamesi and Phoenicoparrus andinus). Zoophagous species that eat invertebrates by the first choice are the dominant group, while in lagoon wetlands phytophages and omnivores are more evenly represented.
Keywords
Birds, diversity, southern Chile, taxonomic distinctiveness

Introduction
Wetlands are defined by the Ramsar Convention (Ramsar 2013) as “areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres”. Five types of wetlands are recognised: Lacustrine, Riverine, Palustrine, Marine and Estuarine (Dugan 1990; Scott and Jones 1995). Inland wetlands are mainly: (a) Lacustrine (e.g. coastal lagoons, lagoons and lakes), (b) Riverine (e.g. waterfalls, rivers, streams, creeks and floodplains) and (c) Palustrine (e.g. bogs, sedge-marshes, fens, shrub-dominated marshes, swamps, seasonally flooded meadows, sloughs, ñadis and marshes). There are also swamp forests, peatlands and man-made wetlands (e.g. reservoirs, dams). Due to its geographical and bio-climatic characteristics, Chile presents many of these types of wetlands (Dugan 1990; Ramírez et al. 1991; Villagrán and Castro 1997; Schlatter and Schlatter 2004; Squeo et al. 2006; Correa-Araneda et al. 2011; Möller and Muñoz-Pedreros 2014; Cepeda-Pizarro et al. 2016). In some cases they combine spatially to form wetland complexes (e.g. with seasonally inundated areas, bogs, riverbeds and/or lagoons).

Wetlands are ecosystems of great biological alpha $\alpha$ diversity, explained by the multiple levels of biological organisation that coexist there, from the genetic composition of many species of different kingdoms to the diversity of environments, considering the structure, function and composition of the elements of biodiversity and their ecological relations (Noss 1990; Kusler et al. 1994; Gibbs 1995; Barbier et al. 1997; Muñoz-Pedreros and Möller 1997). In these ecological relations, assemblages are groups of taxonomically similar species which use different resources but share some components of the habitat, occupying the same space and time (Fauth et al. 1996; Begon et al. 2006). Thus we recognise that a wetland can contain different assemblages which are ecologically interrelated (e.g. assemblages of waterbirds, fish, arthropods and zooplankton); they are therefore ecologically specialised communities in terms of their feeding and use of the habitat, with specific groupings in different types of wetlands (Siegfried 1976; Kantrud and Stewart 1977; Kauppinen 1995). Characterisation of their feeding habits allows us to study guilds within assemblages (see Jaksic 1981; González-Salazar et al. 2014). Wetlands are structurally complex habitats, in which species find sufficient resources for feeding and sites for reproduction (Schlatter and Sielfeld 2006); they also offer a greater alpha $\alpha$ diversity of microhabitats than other ecosystems.

Schlatter and Sielfeld (2006) define waterbirds as those species that are hatched, live, reproduce, feed and/or perish in wetlands; their presence is therefore strictly associated with humid areas (Scott and Carbonell 1986), including the surround-
ing aquatic vegetation. Our target group was the birds of inland wetlands, however various species of waterbirds associated principally with marine wetlands (e.g. plovers, sandpipers, gulls) also use inland wetlands to feed, rest and even reproduce. Likewise, some inland species may use marine areas during some periods of their life cycle or in some parts of the country. Thus the separation between marine and inland waterbirds is only artificial – especially in some parts of Chile – but it can be used to analyse their diversity (alpha $\alpha$ and beta $\beta$), feeding type, use of habitats, etc. (Vilina and Cofré 2006; Vilina et al. 2006).

Birds play important roles in the functioning of these aquatic ecosystems (Martínez 1993), either through their ecological role (e.g., bringing in and consuming nutrients Blanco 1999; seed dispersal Clausen et al. 2002); their value for ecotourism (Klein et al. 1995; Muñoz-Pedreros and Quintana 2010); as bioindicators of environmental changes (Fernández et al. 2005; Amat and Green 2010); or as predators (Gálvez-Bravo and Cassinello 2013). Knowing the structure of a wetland’s waterbird assemblage can provide information about its productivity at the different trophic levels, and the particularities of its structure and functioning (Beltzer 1989). Although the importance of waterbirds is recognised, there are great gaps in information about assemblages of this group in inland wetlands (Victoriano et al. 2006).

Structures of waterbird assemblage must be characterized in order to gauge, using different metrics, the species richness and frequencies in each wetland. In addition, the diversity of these ecosystems should also be studied through an analysis of diversity that includes alpha $\alpha$ diversity: species richness, Shannon-Wiener index, Pielou’s Evenness Index, relative abundance, and taxonomic distinctiveness $\Delta +$, and beta $\beta$ diversity: Bray-Curtis with analysis of similarity percentage.

Our working hypothesis was that the diversity (alpha $\alpha$ and beta $\beta$), of waterbirds differs in different types of inland wetlands. The object of the study was, through a meta-analysis, to identify the structure of waterbird assemblages in a group of inland wetlands, evaluating their richness, diversity, taxonomic structures and trophic guilds.

**Materials and methods**

**Selection of articles**

A meta-analysis allows the results of various studies – related with the object of the analysis – to be combined in order to draw conclusions (Glass 1976). For the present article we considered published information suitable for re-analysis in order to characterise and compare inland waterbird assemblages. The search covered two sources: (a) Bibliographic extraction from Lazo and Silva (1993) and Vega et al. (2011). To complete the information for the years 2012 to 2017, we used (b) Databases, i.e., Scopus, Google Scholar, Center of Environmental and Agrarian Studies Database, using the keywords “waterbirds”, “assemblages” and “Chile” (Boolean operators AND; until 10/23/2017). This search produced 414 records of articles published in peer-
reviewed journals. After the literature survey, we decided on articles specifically focused on waterbirds of inland wetlands based on the title and abstract.

We selected articles from this pool by analysing their reliability, using a mathematical algorithm that we developed based on four variables to determine Eligibility Value (EV), namely: (i) Census method used in the article \( (M) \); (ii) Sampling effort \( (E) \); (iii) Description and precise location of the study area (e.g. geo-referencing, habitat) \( (D) \); and (iv) Type of journal (e.g. with or without editorial committee, indexed) in which it was published \( (R) \). We considered the most important variables to be the Census method and Sampling effort, so they were assigned a greater weighting than the other two variables. The formula used was:

\[
VE = M \times 1 + E \times 1 + D \times 0.5 + R \times 0.25
\]

The weightings assigned to each variable, according to its importance, are indicated. The values ranged between zero and 9.75 (maximum). Articles awarded ≥4 points (close to 50%) were selected for analysis. Table 1 shows the weightings used for each variable. The weightings were assigned by a panel of experts.

### Birds of Chile’s inland wetlands

Schlatter and Sielfeld (2006) recognise 166 species of waterbirds for Chile, with no endemic species, representing 35% of all Chilean bird species. According to Victoriano et al. (2006), excluding the marine ecosystem there are 133 species (29% of the bird species recorded for Chile). For this study we considered waterbirds that inhabit inland wetlands sensu stricto (lacustrine, riverine and palustrine), including species which

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**Table 1.** Factors used to assign Eligibility Value (EV) to the articles found.

| Census method           | Value |
|-------------------------|-------|
| Not described           | 0     |
| Vaguely described       | 1     |
| Partially described     | 2     |
| Completely described    | 3     |

| Sampling effort          | Value |
|--------------------------|-------|
| Single sampling          | 0     |
| Sampling only in the breeding season | 1 |
| Seasonal sampling (at least once in each season) | 2 |
| Annual sampling (at least once per month) | 3 |

| Description of the study area | Value |
|-------------------------------|-------|
| Not described                 | 0     |
| Vaguely described             | 1     |
| Partially described           | 2     |
| Completely described          | 3     |

| Type of journal              | Value |
|-------------------------------|-------|
| Dissemination                 | 0     |
| With editorial committee      | 1     |
| Indexed (e.g. Latindex, Biosis, Zoological Records) | 2 |
| Mainstream (e.g. Ex ISI, Scopus) | 3 |
have a marked relation with aquatic environments and excluding species which do not need aquatic ecosystems for their everyday habits even if they may be observed in these environments (e.g. members of the family Hirundinidae). We also excluded birds considered rare according to the criterion of Barros et al. (2015), who defines as ‘errant’ those species with fewer than five recorded sightings per year; this was determined by analysing recorded information from January 2000 to January 2019 in the scientific publications of the search already described, and of the eBird platform, already filtered (eBird.org). Finally, we drew up a list of inland wetland birds following the systems of Barros et al. (2015) and Remsen et al. (2020).

Analysis of ecological diversity

The information extracted from the selected articles was subjected to diversity analysis, including alpha diversity ($\alpha$), i.e. the diversity of bird species present in each type of wetland, and beta diversity ($\beta$), understood as the degree of change or replacement in species composition between the different types of wetland (Whittaker 1972; Whittaker et al. 2001).

The $\alpha$ diversity was measured by species richness ($S$) and the Shannon-Wiener Diversity Index, which quantifies the total diversity of a sample influenced by two basic components, species richness and evenness. The formula for this function ($p_i \times \log_2 p_i$), where $p_i$ is the proportion of the total number of individuals of the species in question in the sample. The values ranged between zero, when there was only one species, and the maximum ($H'_\text{max}$) corresponding to $\log_2 S$. In addition, Pielou's Evenness Index ($J$) was calculated according to the equation: $J = H'/H'_\text{max}$ (Pielou 1969). This index describes the species evenness of a community, hence it measures the proportion of the observed diversity ($H'$) in relation to the maximum expected diversity ($H'_\text{max}$). Its values fluctuate between 0 (minimum heterogeneity) and 1 (maximum heterogeneity, i.e. the species are equally abundant) (Magurran 1998; Magurran and McGill 2011). We processed this test in a programme created by the authors in an Excel spreadsheet. The relative abundance (AB%), understood as the percentage of the total number of individuals (sensu Krebs 1989), allowed us to identify poorly represented species (low abundance).

To describe the degree of taxonomic relation between the species in each site, we calculated the mean taxonomic distinctiveness ($\Delta+$) (Warwick and Clarke 1995, 1998), understood as an intuitive measure of biological diversity since it considers the mean taxonomic breadth of a sample. To do this we used the taxonomic levels: species, genus, family, order and class, following the classification proposed by Remsen et al. (2020). This index evaluates the species richness together with the taxonomic distance between each pair of species, defined using a Linnaean classification tree. The equation used was: $\Delta + = 2 \sum \sum i \neq j \omega_{ij} (S - 1)$, where $S$ is the number of species in the sample and $\omega_{ij}$ is the distinctive weight or taxonomic distance between species $i$ and $j$ in a taxonomic tree; i.e. each hierarchical level of taxonomy receives a proportional value on a scale of 1 to 100. Thus the value $\omega_{ij}=20$ indicates the same species, $\omega_{ij}=40$ is assigned to differ-
ent species of the same genus, $\omega_{ij}=60$ to different genera of the same family, $ij=80$ to different families of the same order and finally $\omega_{ij}=100$ to different orders of the same class. In other words, the more species belonging to different genera and families there are at a site, the higher the value of $\Delta+$ will be, and therefore the higher the diversity.

To analyse the waterbirds beta diversity, the species abundance data were log-transformed ($x+1$) and generated a Bray-Curtis similarity matrix. Based on similarity hemi-matrices, we obtained an array by non-metric Multidimensional Scaling (MDS) analysis to evaluate and visualise the similarity arrays between sampling points. The similarity-based arrays were also used to generate a cluster analysis between groups, according to the types of environment evaluated. Finally, to identify the species primarily responsible for at least 80% of the bird assemblage structure, we carried out a similarity percentage analysis (SIMPER, Clarke 1993) to quantitatively indicate which birds explain the differences between groups. All the analyses were carried out using the PRIMER-E v6.1.12 software (Clarke and Gorley 2006).

Feeding habits

We grouped the birds into trophic guilds according to their feeding habits, following Martínez (1993): Phytophages (algae and/or macrophytes); Zoophages (invertebrates and/or vertebrates) and Omnivores (phytophagous and zoophagous). Some zoophagous species consume principally invertebrates, and vertebrates only as a second choice (called Ziv); others have plant matter as their second choice (called Zif). Among phytophages, some species consume algae as first choice and macrophytes as second choice (called Fam). Thus the first letter of the code indicates the general classification: zoophagous (Z), phytophagous (F) or omnivorous (O), while the second and third letters indicate the first and second feeding choices (see Martínez 1993) (see Suppl. material 1).

Results

Selection of sources

We identified 22 articles containing information on inland waterbird assemblages in Chile. The Eligibility Value ($EV$) was calculated (Table 2) and 17 were pre-selected ($EV > 4$). Seven of these presented meta-data (information suitable for extraction, tabulation and re-analysis) which we could use in our work; the study areas were distributed among four eco-regions of Chile (sensu Dinerstein et al. 1995). In the Atacama Desert eco-region, Salar de Huasco (Sielfeld et al. 1996) and Laguna Negro Francisco (Oyarzo and Correa 1991); in the Chilean Matorral eco-region, Tranque San Rafael dam (Egli and Aguirre 1995) and Laguna El Peral (Riveros et al. 1981); in the Valdivian Rain Forest eco-region, the wetlands complexes of Lago Lanalhue (Muñoz-Pedreros and Merino 2014) and Río Cruces (Morales and Varela 1985);
and in the Sub-polar *Nothofagus* Forest with Patagonian Steppe eco-region, Laguna de Los Cisnes (Rau 1983). These wetlands fall into four ecosystem types: two High-Andean wetlands (Negro Francisco and Huasco), one man-made wetland (Tranque San Rafael), two wetlands complexes (Río Cruces and Lago Lanalhue) and two lagoon (El Peral and Los Cisnes).

**Birds of inland wetlands**

The list of inland wetland birds consisted of 113 species, as shown in Suppl. material 1; the orders with the greatest representation are the typically aquatic orders like Charadriiformes with 31 species (27.4%), followed by the Anseriformes with 29 species (25.6%). The order Passeriformes presented 15 species (13.2%), more than some exclusively aquatic orders like Gruiformes (10.6%), Pelecaniformes (8.8%), Podicipediformes (4.4%), Phoenicopteriformes (2.6%), Ciconiformes (1.7%) and Suliformes (1.7%). The least represented orders are the Accipitriformes (1.7%), Strigiformes (0.8%) and Coraciformes (0.8%), which consist of species related with aquatic environments only by their feeding habits.

**Alpha diversity**

In the seven sites studied 72 species were recorded (Table 3, Suppl. material 2), with species richness ranging between 12 and 45 species (Table 4). The species richness gradient of the wetlands is as follows: the greatest species richness ($S \geq 30$) was found

| Source                        | M | S | D | T | EV |
|-------------------------------|---|---|---|---|----|
| Aguirre et al. (2007)         | 2 | 4 | 2 | 1 | 7.25 |
| Egli and Aguirre (1995)       | 3 | 4 | 3 | 1 | 8.75 |
| Garay et al. (1991)           | 3 | 4 | 3 | 9 | 9.25 |
| González-Acuña et al. (2004)  | 3 | 4 | 3 | 1 | 8.75 |
| González-Gajardo et al. (2009)| 3 | 1 | 3 | 3 | 6.25 |
| Ibarra et al. (2010)          | 3 | 4 | 3 | 9 | 9.25 |
| Ibarra et al. (2009)          | 3 | 3 | 3 | 8 | 8.25 |
| Kusch et al. (2008)           | 3 | 3 | 3 | 7 | 7.5  |
| Meza (1986)                   | 2 | 1 | 1 | 0 | 3.5  |
| Meza et al. (1999)            | 2 | 4 | 3 | 7 | 7.5  |
| Morales and Varela (1985)     | 3 | 4 | 3 | 0 | 8.5  |
| Muñoz-Pedreros and Merino (2014)| 3 | 4 | 3 | 3 | 9.25 |
| Oyarzo and Correa (1991)      | 2 | 1 | 3 | 4 | 4.5  |
| Rau (1983)                    | 1 | 3 | 1 | 4 | 4.75 |
| Riveros et al. (1981)         | 3 | 4 | 3 | 1 | 8.75 |
| Schlatter (1976)              | 1 | 0 | 3 | 2 | 2.75 |
| Sielfeld et al. (1996)        | 2 | 3 | 3 | 6 | 6.75 |
| Simeone et al. (2008)         | 3 | 4 | 1 | 8.75 |
| Tabilo et al. (2001)          | 2 | 4 | 1 | 6 | 6.75 |
| Tabilo (2006)                 | 0 | 0 | 3 | 1.75|
| Torres-Mura and Lemus (1991)  | 1 | 1 | 3 | 3.75|
in the Río Cruces complex and Tranque San Rafael; medium species richness (S ≤ 29 ≥ 19) was recorded in the Lago Lanalhue complex and Laguna El Peral; and low species richness (S ≤ 18) in the High-Andean wetlands of Negro Francisco and Huasco, and in Laguna de Los Cisnes (Table 4). When the species richness of each site is compared by wetland area, it is interesting to see that the richest wetlands are the smallest (Tranque San Rafael, 1 ha) and the largest (Río Cruces complex, >300,000 ha).

The wetlands presented medium to high evenness values (H’ ≥ 0.58, J ≥ 0.50), except for the Lago Lanalhue complex (H’ < 0.1; J < 0.1) where there was strongly dominant abundance of *C. melancoryphus* (97.7%). The man-made wetland (Tranque San Rafael), which presented the greatest species richness (and the smallest area) also presents high evenness, similar to that of the Río Cruces complex, making it the most diverse of the wetlands studied. Both the High-Andean wetland sites have low species richness and medium/high evenness; their similarity is probably explained by the fact that they are high-altitude ecosystems influenced by similar environmental variables.

**Table 3.** Characterisation of seven inland wetlands in Chile.

| Locality       | HIGH-ANDEAN WETLANDS | MAN-MADE WETLAND | WETLANDS COMPLEX | LAGOON       |
|----------------|----------------------|------------------|------------------|--------------|
|                | Huasco               | Negro Francisco  | Tranque San Rafael | Lago Lanalhue | Río Cruces | El Peral | Los Cisnes |
| Type of wetland| Brackish lagoon and bofedal | Brackish lagoon, bofedal and vega | Dam | Wetlands complexes | Wetlands complexes | Lagoon | Lagoon |
| Location       | Iquique              | Aysen            | Metropolitana     | Biobío        | Valdivia    | Valparaíso | Punta Arenas |
| Coordinates    | 20°15.00'S, 68°50.00'E | 27°26.00'S, 69°15.00'E | 33°16.00'S, 70°53.00'E | 37°55.00'S, 73°17.00'E | 39°42.00'S, 73°12.00'E | 33°30.00'S, 71°36.00'E | 51°01.00'S, 72°52.00'E |
| Altitude (masl)| 3,800                | 4,200            | 498              | 12            | 0           | 9        | 206       |
| Area (ha)      | 6,000                | 1,200            | 1                | 3,100         | 341,407     | 20       | 12        |
| Source         | Sielfeld et al. 1996 | Oyarzo and Correa 1991 | Egli and Aguirre 1995 | Muñoz-Pedreros and Merino 2014 | Morales and Varela 1985 | Riveros et al. 1981 | Rau 1983 |

**Table 4.** α diversity in four types of wetlands in Chile. S= species richness, H’= Shannon-Wiener Index. H’max.= Max. value of Shannon-Wiener Index. J= Pielou’s evenness index. Δ+= Mean taxonomic distinctiveness.

| HIGH-ANDEAN WETLANDS | MAN-MADE WETLAND | WETLANDS COMPLEX | LAGOON |
|----------------------|------------------|------------------|-------|
| Huasco               | Negro Francisco  | Tranque San Rafael | Lago Lanalhue | Río Cruces | Laguna El Peral | Laguna de Los Cisnes |
| S                    | 14 (12.3%)       | 17 (15%)         | 45 (39.8%)    | 20 (17.6%)  | 30 (26.5%)     | 19 (16.8%)      | 12 (10.6%)  |
| H’ (bits)            | 0.58             | 0.63             | 0.94          | 0.08        | 0.94           | 0.82           | 0.77        |
| H’max (bits)         | 1.15             | 1.23             | 1.54          | 1.30        | 1.48           | 1.28           | 1.08        |
| J’                   | 0.50             | 0.52             | 0.61          | 0.06        | 0.63           | 0.64           | 0.71        |
| Δ+ value             | 74.07            | 74.56            | 71.54         | 71.68       | 74.94          | 69.82          | 56.67       |
Beta diversity

The $\beta$ diversity is medium, since the majority of the wetlands (five out of seven) present a similarity greater than 55% and less than 65%; the only sites that are clearly dissimilar are Los Cisnes and the Lago Lanalhue wetlands complex (<35% similarity) (Fig. 1). Two clusters are observed with more than 50% similarity, one consisting of the High-Andean wetlands (64.4% similarity) and the other of Tranque San Rafael, Río Cruces and El Peral (55.8% similarity) (Fig. 2). Similarity percentage analysis (SIMPER) indicates that the greatest contributions to the dissimilarities between the wetlands derive from the species *C. melancoryphus*, *P. jamesi* and *P. andinus* (Table 5); these species present the greatest frequencies in the counts, and between them explain more than 50% of the dissimilarity between the assemblages (Table 5). This explains why the high dissimilarity of the Lago Lanalhue complex is dictated by the high presence of *C. melancoryphus*.

The expected value for taxonomic distinctiveness ($\Delta+$) was 73.2 units. Four wetlands were below this value (Los Cisnes, lago Lanalhue, Tranque San Rafael, El Peral) but within the funnel plot (which expresses the 95% confidence interval). Los Cisnes presented a $\Delta+$ value of 56.67 units, putting it outside the funnel plot, i.e. the weight of the branches of its Linnaean tree is low, meaning that the species that make up this assemblage present lower phylogenetic diversity. The High-Andean wetlands (Negro Francisco and Salar de Huasco) and the Río Cruces wetlands complex were above the expected value; the latter in particular is at the upper limit of the plot with a $\Delta+$ of 74.94 units (Fig. 3), implying that its diversity is the highest of all the sites.

![Figure 1. Bray-Curtis similarity tree diagram of the wetlands analysed. AA= High-Andean wetlands (Huasco and Negro Francisco), HA= man-made wetland (Tranque San Rafael), CH= wetland complexes (Lago Lanalhue and Río Cruces), L= Lakes (El Peral, Los Cines).](image-url)
### Table 5. Analysis of the percentage contribution of species to dissimilarity (SIMPER).

| Species                  | Contrib. % | Cumulative % |
|--------------------------|------------|--------------|
| *Cygnus melancoryphus*   | 19.14      | 19.14        |
| *Phoenicoparrus jamesi*  | 17.68      | 36.82        |
| *Phoenicoparrus andinus* | 14.86      | 51.68        |
| *Anas georgica*          | 9.811      | 61.49        |
| *Fulica armillata*       | 8.242      | 69.73        |
| *Fulica leucoptera*      | 5.379      | 75.11        |
| *Leucophaeus pipixcan*   | 4.073      | 79.19        |
| *Phoenicopterus chilensis* | 3.279      | 82.46        |

### Feeding habits

Seventy-two species of inland waterbirds (64%) are zoophagous (Z); 93% of these consume invertebrates by first choice (Zi), while just five zoophagous species prefer to consume vertebrates (Zv); 22% are omnivorous species (O), of which 72% are phytophagous by first choice (Of); finally, 14% are strictly phytophagous species (F) (see Suppl. material 1). In the High-Andean wetlands, the majority of species are zoophagous (>50%) consuming principally invertebrates (Zi); other zoophagous species consume vertebrates by second choice (Ziv). These groups belong to the families: Recurvirostridae, Charadriidae, Scolopacidae and Laridae. Two phytophagous species (Fa) were also recorded which consume algae (diatoms and unicellular algae), *P. andinus* and *P. jamesi*; they are the only species with this feeding pattern in the assemblages studied.
The man-made wetland Tranque San Rafael presented the largest number of trophic guilds (eight), followed by the wetland complexes and the High-Andean wetlands (seven), Los Cisnes Lagoon (six) and El Peral Lagoon (four). The zoophagous species that consume invertebrates by preference form the majority (>50%) in the wetlands complexes, and in man-made and High-Andean wetlands, while in lagoons more even proportions are found between zoophagous, phytophagous and omnivorous species (Fig. 4).

**Discussion**

**Diversity**

The seven wetlands studied are in different eco-regions (sensu Dinerstein et al. 1995), two in the Atacama Desert eco-region; two in the Chilean Matorral eco-region; two in the Valdivian Rain Forest eco-region; and one in the Sub-polar *Nothofagus* Forest with Patagonian Steppe eco-region. On the other hand, they are different types of wetlands, two High-Andean wetlands, one man-made wetland, two wetlands complexes and two lagoons.
To explain the alpha diversity in the wetlands analysed, we can speculate that the differences between them are linked to the availability of habitats and to productivity: spatial heterogeneity and a dense food supply allow greater trophic specialisation, and thus the presence of a larger number of bird species (Pianka 2000). The authors of the articles analysed did not carry out studies of microhabitats or of food supply; we therefore propose that differences in the species richness (and abundance) of species may be linked to these two factors, without excluding the degree of human intervention (a variable which was likewise not studied). This would suggest that greater alpha diversity.

Figure 4. Feeding types (TA) of the species in the waterbird assemblages of seven inland wetlands in Chile. Z= Zoophagous (i= principally invertebrates; v= principally vertebrates). F=Phytophagous (a= principally algae; m= principally macrophytes). O= Omnivorous (f= principally phytophagous; z= principally zoophagous) (Martínez 1993).
sity of species would be observed in more pristine environments; however the wetland
with the greatest species richness is the man-made wetland, Tranque San Rafael, which
also presents the largest number of trophic guilds.

When we analyse the seven wetlands selected, classified into four types, we deduce
that the most structurally complex environments do not necessarily harbour a larger
number of species, since the diversity of the ecosystem is also subject to the stability
and singularity of the habitats to provide the necessary conditions and sustain a deter-
mined number of species (see Levey 1988; Wiens 1989; Ball and Nudds 1989; Poulin
et al. 1993; Ronchi-Virgolini et al. 2013; Tavares et al. 2015; Lorenzón et al. 2016;
Quiroga et al. 2021). For example, in the Río Cruces and Lago Lanalhue wetlands
complexes, differences were found in the structures of the assemblages, despite the fact
that both are environments with high spatial heterogeneity and low anthropic inter-
vention. This may be explained by the high frequency of the species C. melancoryphus
recorded in Lago Lanalhue (mean 2,200 individuals), resulting in low evenness; this
species migrated from Río Cruces in 2004 when the latter was impacted by a cellulose
plant (see Jaramillo et al. 2007; Muñoz-Pedreros and Merino 2014).

Perspectives for the study of waterbird assemblages

Wetland ecosystems have been rapidly altered and reduced by human activities (Wilen
1989; Gibbs 2000). Wetlands of different origins, such as natural (Dugan 1990), ur-
ban (González-Gajardo et al. 2009) and even agricultural (Czech and Parsons 2002),
are recognised as important environments for waterbirds. Conservation and/or man-
agement of these ecosystems is therefore indispensable. Many of Chile’s wetlands are
not inside protected areas and are subject to strong pressure by economic activities
such as extraction of natural resources and un-programmed and uncontrolled tour-
ism activities (Muñoz-Pedreros and Möller 1997; Schlatter et al. 2001; Möller and
Muñoz-Pedreros 2014). Knowledge of the structure of bird assemblages can help us to
understand how wetlands function, and this information can be used in the generation
of conservation and management plans and programmes.

There are very few studies of inland waterbird assemblages in Chile, and there are
many sites of great importance whose structure and diversity have not been analysed.
Of the wetlands studied, three are Ramsar sites: Salar de Huasco, Laguna Negro Fran-
cisco and Río Cruces (Carlos Anwandter Sanctuary), but the other 13 have few studies,
like other priority wetlands (e.g., Elqui river mouth in the Atacama Desert eco-region,
Rocuant-Andalien marsh and Chamiza wetlands in the Valdivian Rain Forest eco-re-
region). This lack of information hinders the development of proper conservation strat-
egies and programmes for the waterbird assemblages present in inland wetlands. Of
the 17 articles pre-selected, only seven presented meta-data (information suitable for
re-analysis); it is therefore vitally necessary to establish a more demanding protocol for
information-gathering which includes the presentation of meta-data, to allow integral,
standardised analysis. At the same time, specific indices and methodologies should be
applied to the analysis of biological diversity (e.g. α diversity, β diversity, γ diversity;
focal species; fine, medium and coarse filter analysis); functional factors should also be included, and their relation with habitat characteristics. It is important to consider the uses of these indices because the well documented patterns of spatial and temporal variation in diversity continue to stimulate the minds of ecologists today. On the other hand, measures of diversity are frequently seen as indicators of the wellbeing of ecological systems (sensu Magurran 1998).

The diversity consists of not one but two components: the variety and the relative abundance of species, and the indices consider these two aspects. Species richness may only be one component of diversity but it is relatively simple to measure, yet species diversity measures (indices) are often more informative than species counts alone. In the environmental monitoring, diversity measures are widely used and have been extensively tested and prove that diversity measures can be empirically useful (Magurran 1998). All this information would allow the development of a large monitoring program, which together with interconnected citizen science initiatives (e.g., eBird) also contribute to efficient planning of waterfowl conservation.

It is important to explore the need to integrate a type of functional traits among others into the analysis of biological diversity like ecology of feeding. Community studies of inland waterbirds could focus on the guild composition of taxonomic assemblages (see Jaksic 1981; Jaksic and Medel 1990), not simply on species composition, since this provides greater clarity on ecological processes; consideration of the guilds in waterbird assemblages is essential for understanding the role of guilds in the organisation of wetland communities (e.g. Hoeinghaus et al. 2007; Kissling et al. 2011; González-Salazar et al. 2014). All this would allow conservation decisions to be taken based on scientific criteria. The e-Bird bases do not cover the target wetlands. In the future, these citizen records may be used. For now, a meta-analysis based on published studies is one of the best ways to document waterbird assemblages in Chile.

**Author's contributions**

MLM and AMP contributed to the conception and design of the study. AM performed the literature search and/or organised the database. HVN produced the figures and/or tables. MLM and AMP wrote the first draft of the manuscript. AMP and HVN wrote sections of the manuscript. Authors reviewed and/or analysed the literature and contributed to manuscript revision, read, and approved the submitted version.

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**Supplementary material I**

**Supplementary material I**
Authors: María L. Miranda-García, Andrés Muñoz-Pedreros, Heraldo V. Norambuena
Data type: docx file

Explanation note: Birds of Chile’s inland wetlands. Status: P= Species present, NR= Non-breeding, E= Errant (sensu Barros et al. 2015). Feeding: Z= Zoophagous (i= principally invertebrates; v= principally vertebrates). P=Phytophagous (a= principally algae; m= principally macrophytes). O= Omnivorous (p= principally phytophagous; z= principally zoophagous) (sensu Martínez 1993). F = Phytophagous (a = mainly algae; m = mainly macrophytes).

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Link: https://doi.org/10.3897/natureconservation.45.74062.suppl1
Supplementary material 2

Supplementary material 2
Authors: María L. Miranda-García, Andrés Muñoz-Pedreros, Heraldo V. Norambuena
Data type: docx file
Explanation note: Frequency and abundance of waterbirds in seven inland wetlands in Chile.
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Link: https://doi.org/10.3897/natureconservation.45.74062.supp2
Risks and opportunities of assisted colonization: the perspectives of experts

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Academic editor: Chris Margules | Received 4 August 2021 | Accepted 29 October 2021 | Published 15 December 2021

http://zoobank.org/8460DF8B-06EE-4591-9FF7-45BCC8CE397B

Citation: Kracke I, Essl F, Zulka KP, Schindler S (2021) Risks and opportunities of assisted colonization: the perspectives of experts. Nature Conservation 45: 63–84. https://doi.org/10.3897/natureconservation.45.72554

Abstract
Owing to climate change and other anthropogenic environmental changes, the suitability of locations is changing for many biota that consequently have to adapt in situ or to move to other areas. To mitigate the effects of such pressures, assisted colonization is a conservation tool developed to reduce extinction risks by intentionally moving and releasing an organism outside its native range, and thus, to facilitate tracking changing environmental conditions. This conservation tool has been proposed for threatened animals or plants that presumably cannot adapt in situ or follow environmental changes by dispersal or migration. However, there have been contentious debates about the shortcomings and risks of implementing assisted colonization. For this reason, we evaluated the specific opinions of global experts for assisted colonization on potential risks and opportunities that this approach offers. For this purpose, we used an online survey targeted at authors of scientific publications on assisted colonization. The majority (82%) of the 48 respondents were in favor of applying assisted colonization for species that are at risk of global extinction due to anthropogenic environmental change. Most respondents agreed that assisted colonization should be considered only when other conservation tools are not available and that certain preconditions must be met. Some of these were already highlighted in the IUCN guidelines for assisted colonization and include a completed risk assessment, clearly defined management plans and secured political as well as financial support. The advocacy of assisted colonization in response to anthropogenic global environmental changes was only weakly dependent on the geographic origin of the experts and their working background.
Regarding possible risks, most of the respondents were concerned about consequences like failure of the long-term establishment of the translocated species and the transmission of diseases and invasiveness potentially endangering native biota. To keep these risks as low as possible most of the experts agreed that a target area must have a reasonable carrying capacity to sustain a minimum viable population and that adaptive management should be implemented. Careful evaluation of assisted colonization projects is required to generate further evidence that needs to be considered for further developing conservation tools for the Anthropocene.

**Keywords**
Biodiversity conservation, climate change, conservation management, survey, tools, translocation

### Introduction

Climate change is rapidly becoming an increasingly pervasive pressure on species distributions (Dawson et al. 2011; Urban 2015). This novel pressure acts on top of other anthropogenic impacts such as habitat loss, water extraction, toxic pollutants, and invasive alien species (Grimm et al. 2013), which are already threatening the survival of roughly a quarter of extant species (Ma et al. 2018; Díaz et al. 2019). In response to all these unprecedented environmental changes, species are increasingly shifting their ranges (Parmesan and Yohe 2003; Root et al. 2003). Thus, climate change and other anthropogenic pressures create a huge challenge for species conservation and call for the identification of novel tools for ensuring species survival in the Anthropocene (Loss et al. 2011; Wessely et al. 2017; Genovesi and Simberloff 2020).

In general, the survival of species under rapid environmental change will depend on the interplay of in situ adaptation and the capacity of species to track environmental changes in space, i.e. to colonize regions that have become newly suitable (McLachlan et al. 2005; Semenchuk et al. 2021). In situations where in situ adaptation is unlikely, translocation of organisms by assisted colonization may represent an option – at least for some species – (Hällfors et al. 2017; Lloyd et al. 2019) and has been proposed as a novel conservation tool to complement current conservation strategies (Hällfors et al. 2014).

Assisted colonization, also known as assisted migration, managed relocation or benign introduction, is commonly understood as the intentional movement and release of an organism to regions outside its native range (IUCN/SSC 2013). Originally, this conservation tool has been proposed for species whose suitable climatic space is projected to disappear entirely during the next decades in their current range (Hällfors et al. 2017), but for which suitable climatic conditions probably will exist outside their current range. In these cases, future survival may critically depend on species ability to colonize newly suitable climatic space (Minteer and Collins 2010; Ste-Marie et al. 2011). Assisted colonization thus aims to actively support range shifts towards newly suitable regions (Hällfors et al. 2014), and it has been proposed to represent an effective climate change adaptation strategy (Thomas 2011).
Some of the earliest assisted colonization projects were implemented to resolve human-animal conflicts, to increase game populations, and for conservation purposes (Fischer and Lindenmayer 2000). In recent years, an increasing number of assisted colonization events have been implemented worldwide. Examples are the relocation of swamp tortoise (*Pseudemydura umbrina*) in Australia (Seddon et al. 2015), the introduction of the conifer *Torreya taxifolia* in regions north of its current range the USA (McLachlan et al. 2007), and the introduction of two butterfly species (*Melanargia galathea*, *Thymelicus sylvestris*) north of their current range in the United Kingdom (Willis et al. 2009). All these species are assumed to become threatened by climate change in their current range, and thus assisted colonization was deemed to be a useful conservation strategy.

In 2013, the IUCN published official guidelines for conservation translocations of species. There, assisted colonization is defined as the intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species. It is stated that assisted colonization should be carried out primarily where protection from current or likely future threats in the current range is deemed less feasible than at alternative sites. The term assisted colonization includes a wide spectrum of activities, from those involving the movement of organisms to areas that are both distant from the current range and separated by unsuitable areas to those involving small range extensions into areas adjacent to the current range. A recommended feasibility assessment should include a balance of expected conservation benefits against the costs and risks of both the translocation and alternative conservation actions (IUCN/SSC 2013).

Assisted colonization has become a subject of substantial controversy in the conservation community. Contested issues are, for instance, the potential scope and feasibility of this conservation tool, the risks associated with the likelihood of translocated species negatively affecting the biotic environment in their new range, e.g. by becoming invasive, carrying diseases or parasites, and the risk of disrupting historical evolutionary and ecological processes (Hoegh-Guldberg et al. 2008; Ricciardi and Simberloff 2009; Schwartz et al. 2009; Seddon et al. 2009; Minteer and Collins 2010; Loss et al. 2011; Probert et al. 2019). Besides, even if assisted colonization is implemented following a careful risk assessment, it is possible that there are unintended and unpredictable consequences (Ricciardi and Simberloff 2009, 2014), mainly because the impacts of introduced species are highly context-specific and thus substantially vary spatio-temporarily (Ricciardi and Simberloff 2009; Gray et al. 2011). Therefore, some conservationists recommend focusing on traditional conservation tools such as expanding protected areas or improving habitat connectivity (Hunter 2007; Vitt et al. 2009; Javeline et al. 2015).

However, other conservationists argue that assisted colonization involves risks that can be identified ex ante and successfully contained (Sax et al. 2009). For example, it has been argued that adverse effects on native species in the recipient region can be avoided when the focal species is translocated within the same biogeographic region and the target region has no local endemics (Thomas 2011). Another line of argument is that “the consequences of doing nothing would be far worse” than applying a species conservation strat-
egy that has certain limitations (Minteer and Collins 2010). Assisted colonization is also considered as a management tool that fills the gap between species migration capability and the expected velocity of climate change (Ste-Marie et al. 2011). Additionally, assisted colonization is an approach that also encapsulates societal and normative issues (Aubin et al. 2011; Burbidge et al. 2011). Further, solutions for financial, logistical and legal aspects are crucial for successful implementation (Hunter 2007; Hoegh-Guldberg et al. 2008).

Given the diversity of aspects to be considered and the diversity of opinions appearing in the published literature, we evaluated in this study the views of conservation experts on assisted colonization via an online survey. Specifically, experts who had authored scientific articles on assisted colonization in scientific journals were invited to participate in the survey, because the views of scientists working on assisted colonization on different aspects of usefulness and risks of this management strategy are particularly relevant, because they should have the deepest insights and have experienced particular obstacles or risks to be highly important. The questions were dealing with four themes, i.e. usefulness, risks, acceptance, and implementation and a combination of closed and open questions were used in order to obtain both, (i) differences in the proportion of experts agreeing to specific questions and suggested options for answers, and (ii) additional clarifications and recommendations on the aspects addressed. We argue that expert opinions regarding assisted colonization should be influenced by the disciplinary background of experts and their region of origin, because environmental conditions as well as the culture of nature conservation are strongly context-specific. For this reason, we also investigated the role of different backgrounds of respondents (e.g. countries of origin, focal study species) on the attitude towards assisted colonization. Finally, we provide a synthesis of the expert views expressed in this survey and we provide recommendations to take into consideration for future application of assisted colonization.

**Methods**

**Surveying expert opinions**

To assess opinions held on specific issues of environmental management, surveys of expert target groups have been proven effective (Donlan et al. 2010; Javeline et al. 2015; Braun et al. 2016; Pe’er et al. 2017, 2019). Such surveys allow the collection of current knowledge and opinions on specific issues, and if directed towards experts, they facilitate the provision of a synthesis of views held by this target group.

**Identifying the target audience**

For this study, we considered authors of publications on assisted colonization in international scientific journals. Thus, we collected all scientific publications that have dealt with assisted colonization and collected the contact details of the authors. For this purpose, first we researched and evaluated scientific articles in Scopus (www.scopus.com)
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using the term “assisted colonization” and the related search terms “assisted migration”, “conservation strategies”, “relocation”, “moving species”, “translocation of species”, “climate change and threats to species”, “benign introduction”, “risks climate change species”, “reintroduction species”, “climate change impacts on species”.

Secondly, a further selection was made based on titles and abstract, i.e. only articles that dealt with the topic assisted colonization were selected. In addition, “snowballing” was used (Wohlin 2014). Based on the reference lists of the selected articles, additional articles were identified that corresponded with the research criteria mentioned above. Finally, the e-mail addresses of the lead authors and all co-authors and their affiliations were extracted from the articles or researched on the internet.

Overall, the final sample consisted of 264 authors (incl. co-authors) of articles on assisted colonization. They authored 89 articles that were affiliated with 23 countries. Most of these countries lie in the geographical regions of North America, Europe and Oceania. Researchers from these three regions made up 95% of the total sample (Suppl. material 1: Fig. S1a).

Survey design and analysis

In April and May 2019, a web-based survey (www.soscisurvey.de) of expert views on assisted colonization was conducted. The 254 authors were informed by email with an invitation link to participate in the survey. The survey questions were based on previous original research on assisted colonization. For the individual survey questions, Likert-style survey items (Likert 1932) were used – i.e. statements or questions that respondents evaluate from a provided bipolar response scale. Additionally, participating experts could provide open answers and suggestions to some questions.

Overall, the questionnaire contained nine questions with several answer options. The survey questions were divided into five different sections: usefulness, risks and risk mitigation, acceptance, implementation, and summary statements. At the end of the questionnaire, several personal questions were asked to retrieve relevant characteristics of the population of responding experts. In the original survey the term “assisted migration” was used instead of “assisted colonization”. However, throughout this manuscript, we finally applied the term assisted colonization to achieve consistency with the terminology in the IUCN guidelines. The entire questionnaire can be found in the Suppl. material 2.

Data analyses

First, a descriptive analysis of the collected data was carried out to illustrate the responses to the survey questions. Therefore, the response behavior of the respondents is presented in percentage distributions for the Likert-scale categories.

For assessing whether scientists from different parts of the world had differing opinions, the participating experts were assigned according to their affiliations to continents. We tested for significant differences (p-value < 0.05) among the medi-
ans of the different groups using a Kruskal-Wallis one-way ANOVA (McKight and Najab 2010). In the event that a significant difference could be identified among groups, Mann-Whitney U post hoc tests were performed to determine which of the groups differed significantly from the others (Wolf and Best 2010; Bortz and Schuster 2010). Resulting test statistics were converted into Cohen’s d to assess the size of the detected effects.

For assessing whether working background affected the view of experts on assisted colonization, we used the proportions of respondents’ work time allocated for each of the five activities (i) research on assisted colonization, (ii) climate change impacts, (iii) biodiversity, (iv) applied conservation management and (v) conservation policy (see Suppl. material 2) as predictors and the answers to two questions selected from the summary statements (i.e. (i) “Assisted colonization should be recognized as an effective tool for species conservation but with potential risks that need to be carefully addressed” and (ii) ”Assisted colonization should only be implemented if exhaustive assessments are made that conclude that it will not cause a decline in the conservation status of any species native to the target area”) as criteria by conducting correlation analyses using the Spearman rank correlation coefficient. Resulting test statistics were converted into Cohen’s d to enable comparisons of effect sizes with the other statistical tests.

**Results**

**Respondents and their main work fields**

Of 264 invited experts on assisted colonization, 48 (18.2%) participated in the online survey and were assigned according to their place of research to continents (Suppl. material 1: Fig. S1B). Of these, 33 were male, 11 were female, and four respondents gave no information about their gender. The participating experts used an average of 13.2% (±17.0 SD) of their work time in the past five years to conduct research on implementation of assisted colonization. A further 17.4% (±17.2 SD) used to conduct other kinds of research on climate change impacts on biodiversity, and a further 26.9% (±23.3 SD) on yet other kinds of research on biodiversity and nature conservation. The respondents dedicated a further 18.3% (±20.1 SD) of their work time for applied conservation management and 9.2% (±13.3 SD) to conservation policy. A majority of the experts worked on several ecosystems, 59% stated that they worked in forests, 33% worked in grasslands, 26% in mountains, 10% in marine and in urban ecosystems, respectively, 8% in coastal, freshwater and tundra ecosystems, respectively, and 6% in agricultural ecosystems.

**Usefulness of assisted colonization**

The vast majority (85%) of the respondents strongly agreed or agreed that assisted colonization should be considered to be applied when a focal species is threatened
by global extinction caused by climate change and 79% of the respondents strongly agreed or agreed on considering AC when threats are related to anthropogenic pressures other than climate change (e.g. fragmentation, habitat loss, competition, predation, pathogens) (Fig. 1A). There was little agreement for applying assisted colonization for preventing global (27%) species extinction caused by natural causes (e.g. rarity, endemism). For all kinds of threats (climate change, other anthropogenic threats, natural causes), lower agreement values were obtained for preventing regional instead of global species extinction (Fig. 1A).

When asked to select criteria to identify species for assisted colonization, 91% of the experts strongly agreed or agreed that suitable species are those “whose extinction risk could not be reduced despite the implementation of conservation strategies other than assisted colonization” (Fig. 1B). A further 79% strongly agreed or agreed with the application of the criterion extinction risk, expressed e.g. by the Red List status of a species (cf. IUCN 2021). The criteria related to small climatic niches, long generation time when compared to the velocity of climate change, being a keystone species or a species that is relevant for ecosystem functions and for ecosystem service provision received > 67% agreement among respondents. Low genetic variation and phylogenetic uniqueness were considered least relevant (37% and 41% agreement).

**Figure 1.** Answers (n = 48) to the questions A “For which kinds of threats to species, assisted colonization (AC) should be applied?”, and B “Which should be the criteria to identify species for assisted colonization?”.
Risks and risk mitigation of assisted colonization

More than half of the experts considered the three risks of failure, i.e. biotic constraints, abiotic constraints, and human impacts, to be important or very important with only marginal differences among the risks (Fig. 2A). Likewise, the majority of experts estimated specified risks for the native biota of the target area to be of high importance (Fig. 2B); in particular, there was strong agreement on the high importance of transmission of diseases (71%), increased competition with native species (60%), and displacement of native species (58%).

On reducing the risks of failure, 75% of the participating experts held the opinion that selecting a target area with a carrying capacity to sustain a minimum viable population is very important (Fig. 3A), closely followed by measures to implement adaptive management to minimize the risk of failing to establish in the target area (70%) and identifying and protecting climate change refugia for the target species (62%).

When it comes to risk mitigation for native biota in the recipient region, 74% of the respondents stated that the most important aspect was monitoring of the target region and areas adjacent to timely detect negative impacts (Fig. 3B). Other measures, i.e. implementation of adaptive management to minimize the risk for the biota of the

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**Figure 2.** Answers (n = 48) to the questions A “How would you consider the importance of the following potential risks of failure for implementing assisted colonization?”, and B “How would you consider the importance of the following potential risks of assisted colonization for native biota of the target area?"
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Target area and comprehensive and standardized assessment of the potential risks to the biological community of the target area before implementation also received support from a majority of experts (66% and 62%, respectively).

Acceptance and implementation of assisted colonization

A total of 81% of the respondents strongly agreed or agreed that long-term financial and political commitment in the target area is required for assisted colonization projects to be successful (Fig. 4A). A high level of agreement (72%) was also shown for the statement that the political stance including relevant laws and regulation on assisted colonization projects should be assessed. The other three statements (“full authorization by government agencies”, “assessment of citizen attitudes”, “socio-economic impact studies”) were more controversial, but still a majority of respondents (> 56%) agreed or strongly agreed with them (Fig. 4A).

On responsibility for the implementation and related decisions of assisted colonization projects, 83% of the respondents strongly agreed or agreed that government agencies (national to sub-national) should be in charge (Fig. 4B), while it was also widely stated that inter-governmental and multi-national agencies (e.g. IUCN) should take responsibilities (77%). Other stakeholders mentioned by the participating experts were scientists, sub-national government land managers, indigenous peoples, farmers, other landholders, and miners (in the case of restoration sites).
Summary statements on assisted colonization

A total of 82% of the respondents strongly agreed or agreed that assisted colonization should be recognized as an effective tool for species conservation but with potential risks that need to be carefully addressed (Fig. 5). In contrast, the overwhelming majority of experts (83%) denied that assisted colonization is ethically questionable and should be avoided altogether.

Impact of origin on the perception of usefulness and risks of assisted colonization

We found a statistically significant difference among the answers from respondents of different continents on the usefulness of assisted colonization for (i) the prevention of global species extinction caused by anthropogenic pressures other than climate change (Kruskal-Wallis test: n = 48; df = 4; Cohen's d = 0.78; p = 0.046), and (ii) for the prevention of regional species extinction caused by climate change (Kruskal-Wallis test: n = 48; df = 4; Cohen's d = 0.85; p = 0.032). The subsequent post hoc-tests showed that (i) South Americans (median Likert = 2) agreed signifi-
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Significantly less than North Americans (Mann-Whitney U test: n = 19; Cohen’s d = 0.12; p = 0.043) and Oceanians (Mann-Whitney U test: n = 14; Cohen’s d = 1.44; p = 0.032) (median Likert = 4 in both cases) that assisted colonization is useful when globally endangered species are threatened by anthropogenic pressures other than climate change. On question (ii), the post hoc test showed that Oceanians (median Likert = 4.5) agreed significantly more than Europeans (median Likert = 3.5) that assisted colonization should also be considered for the prevention of regional extinctions (Mann-Whitney U test: n = 26; Cohen’s d = 1.92; p = 0.007).

The role of respondents’ working area on the perception of usefulness and risks of assisted colonization

Regarding the dependence of favoring assisted colonization on working time spent on related topics, only one of the ten analyzed correlations was statistically significant. Working time in “research on biodiversity and nature conservation (excluding time for research on assisted colonization and climate change impact on biodiversity)” was negatively correlated (Spearman Rho = -0.32; Cohen’s d = 0.68; p = 0.029) to the agreement with the statement “Assisted colonization should be recognized as an effective tool for species conservation but with potential risks that need to be carefully addressed”.

Discussion

General views on the usefulness of assisted colonization

The expert survey conducted in this study provides a synthesis of the views of world leading experts on assisted colonization. Building on their knowledge, pros and cons of assisted colonization were highlighted. It has to be noted that other target groups (e.g. conservation scientists working in other fields, general public, human populations in...
target regions considered for assisted colonization) might have different views on assisted colonization, which are not considered in this study.

Overall, a substantial majority of participating experts in the present survey were in favor of this conservation strategy and considered assisted colonization as a useful strategy to prevent global species extinction caused by climate change and other anthropogenic pressures. With the publication of the IUCN guidelines on conservation translocations (IUCN/SSC 2013), guidelines regarding risk assessment, regulatory compliance, release strategy, monitoring and management are provided which help to mitigate many of the downsides of assisted colonization. The experts were aware of these possible risks, such as translocated species not being able to establish or threaten native biota. Clearly, assisted colonization should only be applied under certain circumstances. There was a clear difference in the appropriateness of assisted colonization for mitigating natural versus anthropogenic pressures on species. Respondents agreed that to prevent the failure of a translocation, it is crucial that certain precautions are met such as a completed risk assessment, the creation of an adaptive management plan, and detailed monitoring of the target area. Likewise, long-term financial and political support in the target area, as well as relevant legislation are considered essential to successfully implement assisted colonization projects. In view of this, the majority of experts believe that these should be best decided by government- and inter-governmental agencies.

This survey showed that ethical aspects about assisted colonization are considered of modest importance, most likely because protecting threatened species from extinction is considered to be of paramount importance. Nevertheless, ethical considerations in biodiversity conservation in general and assisted colonization in particular require a broad discourse (Minteer and Collins 2005a, 2005b, 2008) with many stakeholders from various part of the society. Taking into account the views of other societal groups might lead to different outcomes but will certainly be necessary when evaluating ethical aspects of assisted colonization. Even among subgroups of the surveyed experts, opinions on assisted colonization differed, with conservation biologists who mainly work on conservation strategies other than assisted colonization being more likely to disagree with assisted colonization. This indicates that perceptions in a broader set of society groups may vary to an even larger degree.

Opportunities of assisted colonization

Most of the respondents stated that assisted colonization is an appropriate conservation measure to prevent global species extinction caused by climate change and other anthropogenic pressures (e.g. fragmentation, habitat loss, pathogens). The prevention of global species extinction threatened by climate change seems to be the main justification of the respondents of this survey for applying assisted colonization. In the first two decades of the 21st century, the impacts of unfolding climate change on biodiversity have become an urgent global concern (Williams et al. 2003; Deb et al. 2018). However, the experts in the present survey considered assisted colonization not only as a means to overcome barriers that hinder range shifts required to match climatic re-
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Requirements of populations (Javeline et al. 2015), but also to prevent extinction caused by other anthropogenic pressures than climate change. This finding reflects the insight that the unfolding global extinction crisis is caused by several interacting pressures (IPBES 2019; Otero et al. 2020).

Previous studies have shown that other conservation strategies (e.g. expanding protected areas, the establishment of corridors, ex situ conservation) are preferred to assisted colonization (Javeline et al. 2015). This view is generally supported by the respondents of this survey, in particular when dealing with threats that are not related to anthropogenic influence or with extinctions at regional level. However, these conservation strategies might not be effective enough to cope with climate change in strongly fragmented landscapes (Wessely et al. 2017). Thus, there is an urgent need to assess critically all potentially applicable conservation strategies (Genovesi and Simberloff 2020).

The analysis showed that most respondents (79%) considered the use of assisted colonization only appropriate for highly threatened species. In another question, 91% of respondents viewed assisted colonization only appropriate in cases that cannot be effectively solved by other conservation strategies. Clearly, assisted colonization should be used as the method of last resort. An example could be the Pyrenean desman Galemys pyrenaicus, a semi-aquatic mammal of the family Talpidae inhabiting a small range in northern Spain and Portugal. Climate modelling indicates that this species, already threatened by several pressures, might not survive climate change in its current range (Morueta-Holme et al. 2010). However, streams in western Britain might be suitable habitats for the species (Thomas 2011).

According to the results, the protection status of a species seems not to be the only relevant criterion. Other criteria that were considered relevant such as small climatic niches, poor dispersal capacity compared to the velocity of climate change (Loarie et al. 2009), being a keystone species or a species that is relevant for ecosystem service provision should be taken into account in decisions as to whether a species is suitable for assisted colonization (Hällfors et al. 2017). The importance of species values and the importance of ecological functional properties indicate that different and sometimes competing motivational goals exist to select a species for assisted colonization (Aubin et al. 2011; Hagerman and Satterfield 2014). Thus, fundamental perspectives on nature and causes of its endangerment seem to influence the opinions of experts on assisted colonization (Aubin et al. 2011; Burbidge et al. 2011; Ste-Marie et al. 2011).

Oceanian experts were strongest in favor of applying assisted colonization for the prevention of regional (i.e. as opposed to global) species extinctions. This is probably related to Oceania’s distinct insular biogeography, which results in a particularly large number of highly threatened species and the related urgency for applying and testing novel conservation measures (Short 2009; Burbidge et al. 2011; Seddon et al. 2015).

Risks of assisted colonization

Experts were most concerned about failure of the long-term establishment of the translocated species caused by biotic constraints (e.g. competition, predation, parasitism) in
the target region. This reflects the difficulty of assessing certain crucial parameters that are essential for planning and implementing assisted colonization projects such as (i) species-specific sensitivity to climate change, dispersal abilities, habitat requirements, habitat availability, (ii) information pertaining to the target region (e.g. biotic interactions among species, land ownership), and (iii) uncertainty about future environmental and climate change trajectories (Hällfors et al. 2017). Each candidate species should be evaluated carefully to judge the balance between potential benefits of helping to save a species from extinction and potential risks to native biota within the recipient area (Thomas 2011). Several systematic processes are suggested for identifying potentially suitable sites for translocation. For instance, multiple criteria analysis (MCA) facilitates the assessment on whether (i) assisted colonization is well planned and monitored, (ii) could be a possible contribution to achieve conservation goals and (iii) will ultimately result in the establishment of long-term sustainable populations (Carroll et al. 2009; Miller et al. 2012; Dade et al. 2014).

The results of our survey showed that a rather high percentage of experts were concerned about the transmission of diseases and, more generally, the emergence of invasive behavior in the recipient region potentially threatening native biota. For instance, the potential invasive spread of the target species and unforeseen pathogen transmission to native species in the recipient region are plausible and potentially highly impactful scenarios (Aubin et al. 2011; Pedlar et al. 2012; Ferrarini et al. 2016). From invasion science it is well-known that the transport of animals and plants by humans spreads disease-causing pathogens (Collins and Crump 2009; Rabitsch et al. 2017) and promotes the spillover to new host species (Slippers et al. 2005). Assisted colonization may entail similar risks. An example is the introduction of the American red squirrel Tamiasciurus hudsonicus into Newfoundland. Assisted colonization was done partly to improve the diet of the pine marten (Martes americana), a declining species. However, a previously unexpected competition with birds for black spruce cones as a food resource developed, which might have resulted in the decline of the Newfoundland red crossbill (Loxia curvirostra perna) (Schwartz 2005). Several respondents expressed concerns over the potential impacts of translocated species on cultural and aesthetic values of the recipient region particularly if they potentially become conspicuous or abundant (Palmer and Larson 2014). On the other side, the loss of a species in its original range also may affect cultural values (Sandler 2013; Palmer and Larson 2014). Assisted colonization cannot fully restore such context-specific values, but preserving a species offers the opportunity to preserve the values attached to the species in question.

Reducing risks of assisted colonization projects

This study showed that the following measures are considered most relevant by the respondents to enable successful assisted colonization: (i) selecting a target area with a carrying capacity large enough to sustain a minimum viable population, (ii) identification and protection of climate change refugia, and (iii) implementation of adaptive management to minimize the risk that the migrant population fails to establish in the target area.
As a necessity to justify assisted colonization as an effective conservation tool, careful study, risk management, and supported implementation are essential (Mueller and Hellmann 2008). Of particular importance for the success of assisted colonization projects is assessing habitat suitability and availability to the needs of the candidate species (IUCN/SSC 2013). The determination of carrying capacity and estimates on climate change refugia are additional crucial criteria for identifying suitable regions for the translocated species and to ensure successful establishment (Hällfors et al. 2017). For instance, climate models that show future climate changes in relation to the tolerance limits of species could be a useful tool to obtain appropriate information (IUCN/SSC 2013). Further, in the case of translocation by assisted colonization, the implementation of management measures is essential and depends on monitoring results, which create the basis for progressive or adaptive management measures.

In order to minimize negative effects on native biota, a majority of the respondents considered that one of the most relevant activities should be monitoring of the target region and adjacent areas to identify potential negative impacts. The IUCN/SSC (2013) guidelines highlight that monitoring in the course of a translocation is essential. Thus, before the implementation of an assisted colonization project, it is important to evaluate the effects of future climate scenarios on ecological and hydrological processes of the recipient ecosystem (Carroll et al. 2009), to monitor target species and their social environment (Schwartz and Martin 2013) and to evaluate the predictions through species distribution models (Hällfors et al. 2017). This also includes monitoring to identify new threats to the translocated population which were not part of translocation design to minimize the risk that the translocated population fails to establish in the target area (IUCN/SSC 2013). Finally, assessing and monitoring demography, behavior, ecological functions, genetics, health conditions and mortality, social, cultural, and economic interest of the translocated species are important (IUCN/SSC 2013).

Acceptance and implementation of assisted colonization

Evidently, assisted colonization has to comply with laws and international regulations, e. g. with the World Organisation for Animal Health standards for animal movement and those of the International Plant Protection Convention (IUCN/SSC 2013). Compatibility with logistic constraints on land use in the target regions need to be taken into account (IUCN/SSC 2013). But beyond logistic aspects, further implementation criteria need to be considered.

A large majority of experts considered secured financial and political commitment and appropriate regulatory frameworks as necessary preconditions for implementing assisted colonization. Costs for implementing assisted colonization are highly context-specific and can result from a wide array of measures such as captive breeding of the target species, monitoring, and land purchase (Pedlar et al. 2012). The IUCN/SSC (2013) guidelines highlight that there should be awareness of possible needs for funding from any damage caused by the translocated species. Furthermore, flexible budget
plans should be available to allow for adaptive changes to an assisted colonization project during implementation.

In terms of responsibility for the implementation and related decisions of assisted colonization projects, most of the respondents held the opinion that this should be the task of government agencies and inter-governmental and multi-national agencies (e.g. IUCN). Government agencies and multinational agencies should not only assume responsibility but should also collaborate intensively with conservation science to identify potential benefits and risks that could become important contributions for advancing the development standards and guidelines for assisted colonization (Javeline et al. 2015). Further, cooperation between the various stakeholders is needed to minimize the risk of poor implementation of assisted colonization projects (Javeline et al. 2015).

Conclusions

While it is clear that assisted colonization is a conservation tool that can only be applied to a rather limited number of species, this study reveals substantial backing from the surveyed conservation experts for improving the survival prospects of threatened species by assisted colonization as a useful conservation strategy under rapid environmental change, when other conservation strategies are not an available option. Experts most strongly support assisted colonization for pressures related to climate change, but also are in favor of assisted colonization as a management option for other anthropogenic threats. However, experts clearly expressed concerns on possible risks and negative consequences that are inherent to assisted colonization. Therefore, the approval of this conservation method is bound by several requirements such as (i) a collection of precise species-specific data of needs and conditions, (ii) a completed exhaustive risk assessment, (iii) a clarification of any legal or financial obstacles, (iv) implementation of previously defined management measures, and (v) further monitoring of target areas to successfully establish the translocated species while protecting native biota. Accordingly, reducing the risks caused by possible disease and pathogen transmissions, potential invasiveness of the translocated species and failure of long establishment are required.

Acknowledgements

We are grateful to all the experts who have supported this study by completing the survey. The contributions by K.P.Z. and S.S. were funded by the Austrian Climate and Energy Fund within the framework of the “Austrian Climate Research Programme” (Project “Conservation under Climate Change: Challenges, Constraints and Solutions”; Number KR17AC0K13678). FE was funded through the 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme with Project “Alien Scenarios” (FWF project no I 4011-B32). We appreciate the comments of two anonymous reviewers that helped to improve the manuscript.
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**Supplementary material 1**

**Figure S1**
Authors: Irma Kracke, Franz Essl, Klaus Peter Zulka, Stefan Schindler  
Data type: Figure (docx. file)  
Explanation note: Figure S1. Geographical affiliation of (a) the authors of scientific articles (n = 264) on assisted colonization (assignment of the lead authors and co-authors was done based on Internet research at which institute they carried out their research), and of (b) the authors of scientific articles who took part in the survey (n = 48) on assisted colonization.  
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Link: https://doi.org/10.3897/natureconservation.45.72554.suppl1

**Supplementary material 2**

**The questions used in the online survey**
Authors: Irma Kracke, Franz Essl, Klaus Peter Zulka, Stefan Schindler  
Data type: docx. file  
Explanation note: The questions used in the online survey.  
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Link: https://doi.org/10.3897/natureconservation.45.72554.suppl2