RESEARCH ARTICLE



Orchid conservation and research: An analysis of gaps and priorities for globally Red Listed species

Jenna Wraith D, Patrick Norman, Catherine Pickering

Received: 21 August 2019/Revised: 29 October 2019/Accepted: 6 December 2019/Published online: 20 January 2020

Abstract Orchids are among the most threatened taxa globally due to increasing anthropogenic threats, inherent rarity and specific conservation needs. But what are the global research and conservation priorities for this charismatic group of plants? Using information for 595 orchids on the IUCN Red List, we reviewed past research and identified key research and conservation priorities. These included understanding threats, monitoring orchid populations and habitats, species management in ex situ conservation, genome resource banks and artificial propagation, land and habitat protection and education and awareness through communication. Based on the available data, we recommend future orchid conservation and research should focus on the current gaps in knowledge and practice including monitoring population trends and distributions, ecology, threats, protection and management of species and their habitats and increasing education and awareness.

Keywords Anthropogenic threats · Conservation · Global biodiversity · IUCN Red List · Threatened species

INTRODUCTION

Species conservation is increasingly important globally as biodiversity is declining rapidly, with over a million species currently threatened with extinction (Ceballos et al. 2010, 2015; Díaz et al. 2019). Threats to global biodiversity are widespread, diverse and mostly stem from anthropogenic activities such habitat loss as a result of land clearing and development, climate change, pollution and over-exploitation (Brook et al. 2008; Stork 2010; Hanski 2011; Urban 2015; Valiente-Banuet et al. 2015; Díaz et al. 2019). The rate at which species are declining is only increasing as is the scale and extent of threats (Larsen et al. 2011; Wraith and Pickering 2019). With such a time crisis, it is critical that we prioritise research and conservation, including for at risk taxa such as orchids (Larsen et al. 2011).

Orchids are highly diverse with over 27 000 species in \sim 1000 genera with populations found on all continents across the globe other than Antarctica (Swarts and Dixon 2009a). They occupy a vast range of habitats from high alpine tundra to tropical rainforests, with their success in part attributed to their ability to grow in the soil (terrestrial form), on trees (epiphytic form) or on rocks (lithophytic form). However, they are also one of the worlds most threatened taxonomic groups (Wraith and Pickering 2018) with over 600 species of orchids listed as threatened on the global database of threatened species maintained by the International Union for the Conservation of Nature, known as the IUCN Red List (IUCN 2019).

The threatened status of many orchids is partly a result of their intrinsic rarity due to factors such as small population sizes, limited distributions and species-specific symbioses with pollinators and mycorrhizal fungi (Swarts and Dixon 2009a; Seaton et al. 2013). This creates a complex ecology that relies on the success of a range of species-specific interactions and abiotic factors which are being eroded by climate change, habitat modification and altered land use (Swarts and Dixon 2009a; Liu et al. 2010a; Seaton et al. 2010; Wraith and Pickering 2019). These threats, along with increasing impacts of invasive species, changes in fire regimes and illegal collecting are the most common threats to orchids globally and often co-occur as threat syndromes (Wraith and Pickering 2018, 2019). Orchids are highly charismatic, with a long history as the objects of desire for collectors, contributing to population and species declines (Ghorbani et al. 2014; Hinsley et al. 2017b; Wraith and Pickering 2017). Due to the specialised biotic factors and threat syndromes, successful conservation of orchids in the wild is often difficult and requires the input of a range of research disciplines.

Historically research on orchid conservation has focused on taxonomy including identifying and describing new species (Swarts and Dixon 2009a). More recently with emerging technology there has been a shift in research examining the molecular biology of orchids, including orchid mycorrhizal associations (Liu et al. 2010b; McCormick et al. 2012; McCormick and Jacquemyn 2014) contributing to conservation by facilitating successful propagation of many threatened orchids. Other emerging research fields in orchid conservation include pollination biology, species distributions and methods for translocating orchids for both in situ and ex situ conservation. As the success of orchid conservation relies on all these fields, an integrated approach has been suggested to incorporate factors such as threats with speciesspecific associations, and ex situ and in situ conservation (Swarts and Dixon 2009a; Liu et al. 2010b).

With orchid numbers continuing to decline in most regions globally (Fay 2018; Wraith and Pickering 2018, 2019), it is important to review current research, and identify research priorities and conservation goals. We assist this process using data from the IUCN Red List and other sources to answer the following questions: (1) What are the trends in orchid conservation research? (2) What are key research priorities for orchid conservation globally? (3) What are the key conservation priorities for threatened orchids globally? (4) What factors influenced conservation priorities?

MATERIALS AND METHODS

Data collection

To determine trends in orchid conservation research, bibliometric data were collected from the online academic literature database Scopus in July 2019. This well-regarded database covers ~ 70 million publications globally and can be searched using keywords and authors (Martín-Martín et al. 2018). Scopus was searched for all articles and reviews containing the terms orchid, orchids or Orchidaceae and conservation, conserve or conserved in the title, abstract or key words. The search was limited to English only publications and excluded publications that did not relate to orchid plants including those in medicine and pharmacology, toxicology and pharmaceutics. Information on publications was downloaded from Scopus including authors names, the organisations they are associated with, including in which countries, the year published, publisher, source and author keywords.

To assess global research and conservation priorities for threatened orchids, data were collected from the IUCN Red List in May 2019. It was searched for all threatened orchids listed as critically endangered (CR), endangered (EN) and vulnerable (VU) and then data transferred over into a personal database. This included taxonomic data for all 595 orchid species listed as CR, EN and VU (IUCN 2019). Additional data included information for each species, threats, land regions and growth form as well as all listed research priorities (three broad categories and 13 subcategories) and conservation priorities (six broad categories and 36 subcategories) (Fig. 1). Then to determine if there were taxonomic patterns in the data, the tribes for each genus were included using data from the NCBI taxonomy database and accompanying literature (Sayers et al. 2009).

To highlight spatial patterns in conservation priorities, data on the distribution of each of the species were collected where available. This included 18 464 occurrence records for 565 of the 595 threatened orchid species from the Global Biodiversity Information Facility (GBIF 2019) obtained using the rgbif package using R and RStudio (RStudioTeam 2016; Chamberlain et al. 2019; R Core Team 2019). After removing duplicates, occurrences with missing or suspect coordinates and those collected before 1969, the total data were reduced to 6471 unique occurrence records covering 432 species.

Data analysis

To highlight trends in orchid conservation research, the bibliometric data from Scopus were analysed and the results visually presented as networks using VOSviewer software tool which supports in constructing and visualising bibliometric networks (Centre for Science and Technology Studies 2019). Specifically, we analysed cooccurrences of all keywords listed by authors that occurred in 10 or more publications. For threatened orchids on the IUCN Red List, descriptive statistics were calculated to identify the most common research and conservation actions listed for the most common orchid tribes. Chisquare (γ^2) analyses were conducted to determine if there were significant differences in Conservation status depending on the tribe using R (R Core Team 2019). Bray-Curtis cluster analyses were then conducted to determine patterns between threats to orchids and specific conservation priorities (Clarke and Gorley 2006).

To determine the geographical pattern in threatened orchids and conservation priorities, occurrence records for each species were linked with the corresponding conservation priorities using R (R Core Team 2019). Then species richness of threatened orchids was calculated per country and mapped using QGIS (QGIS Development Team 2019). Finally, pie charts showing conservation priorities were overlayed for the 20 counties with the largest number of threatened orchids.

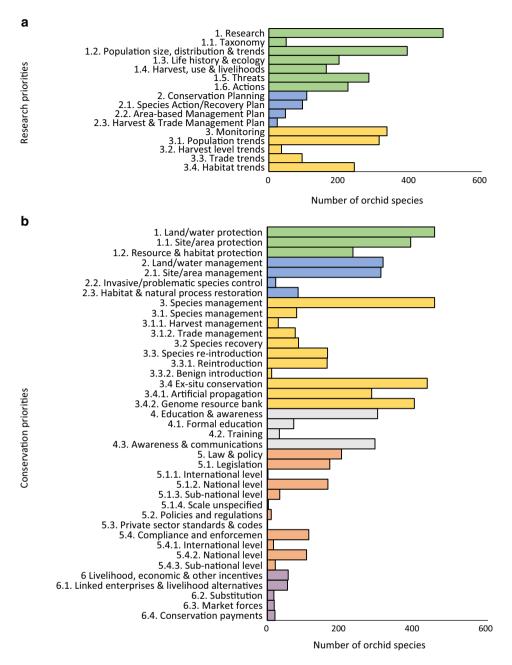


Fig. 1 A summary of the 491 threatened orchids on the IUCN Red List for and **a** their future research priorities (1-3) and subcategories and **b** their conservation priorities (1-6) and subcategories

RESULTS

What are the trends in orchid conservation research?

Research on orchid conservation had increased over the past 20 years, but mainly in the last few years with an average of 118 publications per year from 2010 to 2018 (Fig. 2a). The overall literature is large with 1449 documents published since 1969 and is diverse in terms of the range of authors, where they are from, and the topics they

examined. For example, authors from more than 93 countries have contributed to the literature, but many authors are from the United States of America (17%), Brazil (12%), China (11%), the United Kingdom (10%) or Australia (9%). Some organisations were heavily involved in orchid research including the Royal Botanic Gardens, Kew in the United Kingdom, which is responsible for 6% of the publications, while the Chinese Academy of Sciences (5.5%), the University of Western Australia (3%), the University of Florida in the USA (2%) and Kings Park and Botanic Gardens, also in Western Australia (2%) have also

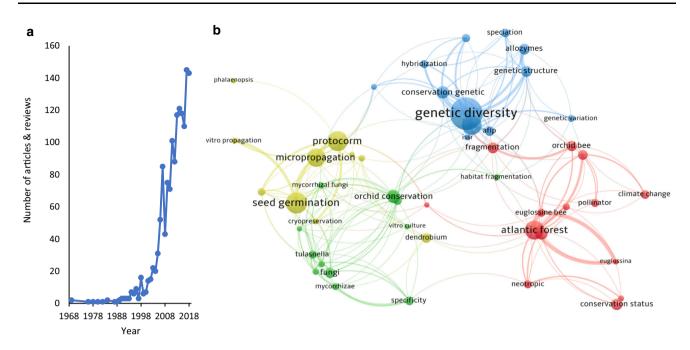


Fig. 2 The number of research articles per year (a) and common themes in orchid conservation based on author keywords (b) using data from Scopus

contributed. Orchid conservation attracts a wide range of researchers with more than 150 authors authoring four or more publications, and one author, K. Dixon, authoring 2% of all the research. In terms of disciplines, research was mainly in agricultural and biological sciences (1270 articles), biochemistry, genetics and molecular biology (338) and environmental science (314).

There were four broad themes to orchid research to date: genetics, fungi, propagation and pollination (Fig. 2b). Genetic research included conservation and population genetics, genetic structure and microsatellite markers and was linked with research on the mycorrhizal fungi of terrestrial and epiphytic orchids. Much of the research on fungi examined species-specific interactions between fungi and orchids, including the fungal genus, *Tulasnella*. A second theme was orchid propagation including seed germination, protocorms, micropropagation including *Phalaenopsis* orchids. Research on pollination focussed on specific orchids and/or euglossine bees, with many articles conducted in the Atlantic forest of Brazil. Less common was research on habitat fragmentation and climate change.

What are key research priorities for orchid conservation globally?

Research is a priority for 82.5% of the 595 orchids on the IUCN Red List. Most often this was research on population size, distribution and trends (390 species). Research on threats (282) and potential actions (223) were also important, in contrast to taxonomy which was only listed for 49

species. Monitoring was a priority for 333 species with the monitoring of populations (311) and habitats (241) commonly listed. Research on conservation planning was a priority for 107 species with species action and recovery plans the main focus (97) (Fig. 1a).

What are the key conservation priorities for threatened orchids globally?

The four main conservation priorities for orchids were (1) land/water protection (455 species), (2) land/water management (309), (3) species management (455) and (4) education and awareness (300) (Fig. 1b). At a finer scale (sub categories), the most common priorities were species management in ex situ conservation (435 species), genome resource banks (400) and artificial propagation (284), land protection for the site/area (233) and habitat protection (233), management for the site/area (309) and education and awareness through communications (293).

What factors influenced conservation priorities?

There were clear patterns in the taxonomic affiliation of orchids on the Red List. Although orchids on the IUCN Red List represent 26 different tribes, most on the list belong to one of six tribes. The most common was Vandeae (116 species) and Orchideae (93), most of which were endangered. Cypripedilinae (84) were mostly critically endangered, Dendrobieae (77) were most vulnerable, Cypripedieae (47) were mostly endangered, and Epidendreae (34 species) included some vulnerable, some endangered and some critically endangered species (Table 1). As a result, the proportion of species listed as critically endangered, endangered and vulnerable varied significantly among these six orchid tribes (χ^2 test, p < 0.001).

There was a complex relationship between orchid tribes and conservation priorities (Fig. 3). Priorities for orchids from the Cypripedieae were diverse and included land management, education and awareness, land protection, law and policy, species management and economic incentives. For orchids from Cypripedilinae, Dendrobieae and Vandeae, there were similar priorities, although economic incentives were less important. In contrast, economic incentives were less important for orchids in Epidendreae, Malaxideae and Phragmipedieae. For some tribes, there were specific priorities, such as for Cranichideae orchids land protection and management were the main priorities for conservation.

There were clear links between certain types of threats and conservation priorities for the orchids (Fig. 4). For orchids threatened by biological resource use, conservation priorities included land management (75% similarity), protection (93% similarity) and species management (93% similarity). For orchids threatened by human intrusion and disturbance, conservation priorities included education and awareness, law and policy (75% similarity). For orchids threatened by pollution, conservation priorities included livelihood, economic and other incentives (76% similarity), which were also important for orchids threatened by climate change and severe weather (55% similarity) and transportation and service corridors (65% similarity) (Fig. 4).

Although conservation priorities for orchids varied among many countries and regions, for most countries with many threatened orchids, land protection was important (Fig. 5). Madagascar, China, Vietnam, United States of America and Mexico have the largest number of threatened orchids and vary in their conservation priorities (Fig. 5).

Table 1 Orchid tribes with the largest number of species on the IUCN Red List and their specific conservation status which varied significantly among each of the orchid tribes (χ^2 , p < 0.001)

	Vulnerable	Endangered	Critically endangered	Total
Vandeae	19	64	33	116
Orchideae	15	49	29	93
Cypripedilinae	2	37	45	84
Dendrobieae	31	28	18	77
Cypripedieae	13	22	6	41
Epidendreae	10	15	9	34

Land protection and species management were important for orchids in Madagascar, as was land management, education and awareness, while livelihood, economic and other incentives as well as law and policy were not important. For orchids in China, Vietnam and most countries in South East Asia all six conservation priorities were important, while for orchids in North America and Canada, land protection and management, law and policy, species management and education were most important. Conservation priorities for orchids in Mexico included land protection, law and policy and education and awareness, while for orchids in South America and Australia livelihood, economic and other incentives were not as important (Fig. 5).

DISCUSSION

Current research on orchid conservation

With orchids declining due to threats such as habitat loss, climate change and illegal collecting, research on orchids including their conservation is crucial (Reiter et al. 2016; Fay 2018; Wraith and Pickering 2018). Positively, research on orchid conservation has increased including due to the work of a wide range of researchers from many countries and institutions and as a result there is now a large body of literature, most produced in the last 10 years. To date, most of the research has focussed on (1) genetics and taxonomy, (2) mycorrhizal associations, (3) propagation and (4) pollination, which all contribute to orchid conservation.

The focus on research into genetic diversity, structure and variation in orchids has been vital for understanding orchid taxonomy, population viability and the threatened status of species contributing to the development of appropriate conservation priorities (Case et al. 1998; Chung et al. 2004; Forrest et al. 2004; Pillon et al. 2007; Swarts and Dixon 2009a; Swarts et al. 2009; Fay 2018). Studies have successfully linked factors such as a lack of gene flow and increasing levels of inbreeding with threatening processes, highlighting the negative effects of habitat fragmentation as seen for Australian threatened orchids such as Caladenia huegelii and Phaius australis (Swarts et al. 2009; Simmons et al. 2018). Our knowledge of mycorrhizal associations has increased with the development of molecular techniques such as DNA sequencing. This includes information about fungal associates within the genus Tulasnella and Rhizoctonia that are important for the survival of many rare and endangered terrestrial species (Linde et al. 2017; Reiter et al. 2018). Understanding mycorrhiza associations is particularly important as orchids, unlike most other plants, rely on these relationships for

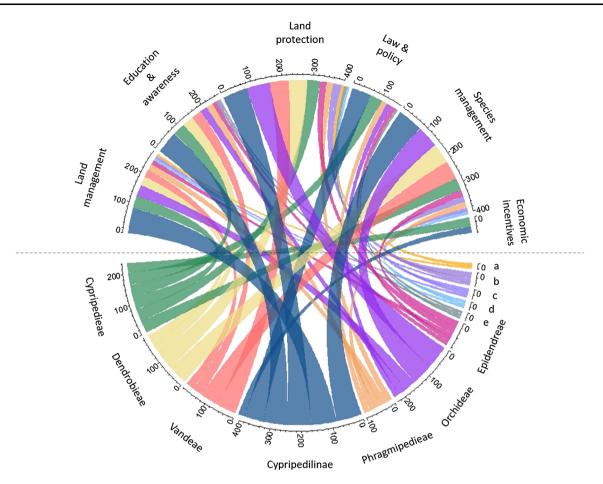


Fig. 3 Number of orchids per tribe (bottom) compared to the listed conservation priorities (top) based on data from the IUCN Red List, displayed as a chord diagram created using the circlize package in R (Zuguang et al. 2014). Tribes with few species are labelled as a Cranichideae (yellow), b Cymbidieae (dark purple), c Malaxideae (light purple), d Neottieae (light blue), and e Vanilleae (khaki)

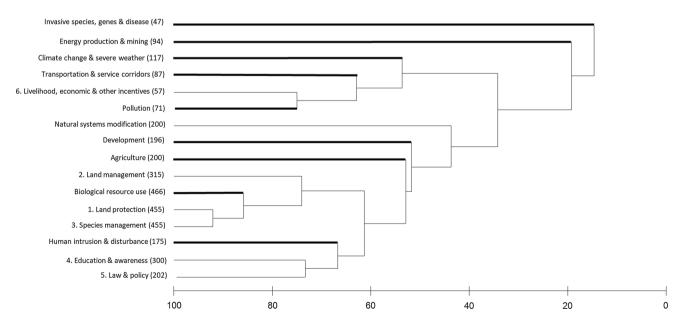


Fig. 4 The relationship between the most commonly listed threats (bold lines) and listed conservation priorities (narrow lines) for orchids on the IUCN Red List. Data were analysed using Bray–Curtis cluster analysis (similarity) for threats and conservation priorities affecting over 20 species with the number of species in parentheses

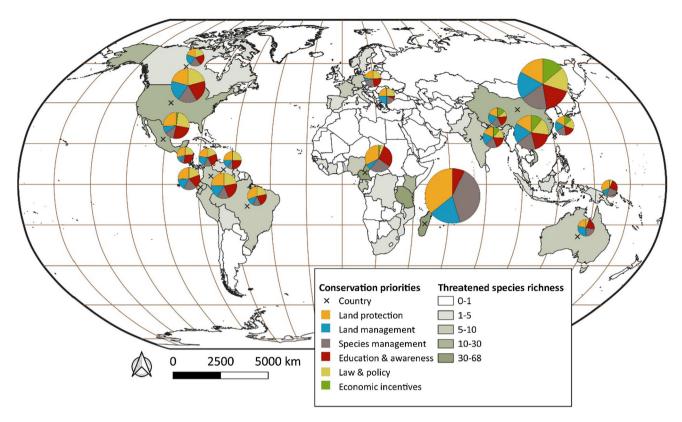


Fig. 5 Global pattern is species richness of threatened orchids on the IUCN Red List and their associated conservation priorities (pie charts) for the 20 countries with the largest number of threatened orchids

seed germination (Swarts and Dixon 2009b; Yeung 2017; Fay 2018).

Seed germination is one of the most important, yet inherently difficult, challenges in orchid conservation (Reiter et al. 2016). For many orchids, ex situ conservation is important, and the propagation relies on artificial seed germination and therefore mycorrhizal research, for success (Swarts and Dixon 2009b; Reiter et al. 2016). Recently research has focused on protocorm development and cryopreservation techniques particularly for Dendrobium and Phalaenopsis and other attractive species in horticulture, as well as other threatened orchids (Liu et al. 2010b). Propagation including germination is also important for translocations and/or re-introduction of species into natural habitats. For successful re-introductions, information on many aspects of the orchid's ecology is required including the role of pollinators (Reiter et al. 2016, 2017; Brundrett 2019). Research into pollination has focused mainly on euglossine bees. Although interesting, focussing on this one group of orchids and pollinators that only occur in South and Central America is not always useful for orchid conservation more broadly. Research on pollinators in other regions would be valuable as highly specific pollination syndromes in orchids remain an important issue in conservation (Peakall et al. 2010; Phillips et al. 2015; Reiter et al. 2017) and the loss of pollinators is often listed as a key threat (Wraith and Pickering 2018). More research on pollination strategies, pollinator species and their distributions facilitate the success of many more orchid reintroductions and translocations (Phillips et al. 2015; Reiter et al. 2017).

Research priorities

Our analysis of orchids on the IUCN Red List highlighted four major research priorities. The most frequently listed research priority was understanding orchid population sizes, distributions and trends. This includes research on species distribution modelling and the impacts of climatic change, which has not been a major focus of research to date. Monitoring populations and their habitats is another priority and requires field surveys and long-term habitat assessments (Kull et al. 2008; Liu et al. 2010a). The ecology and life history of orchids is complex and an important priority for conservation research, with specific associations between many orchid species and specific mycorrhizae, pollinators, seed dispersal (Swarts and Dixon 2009a; Reiter et al. 2018). Understanding key threats to orchids and identifying practical solutions to eliminate or mitigate threats is a high priority for orchid conservation. For instance, many orchids are affected by habitat loss from development, agriculture, roads, forestry, grazing, fire and illegal collection, but there

are other less common threats that need further investigation, including the impact of small population sizes, loss of pollinators and climate change (Wraith and Pickering 2018, 2019). The least important research priority for orchids on the IUCN Red List was taxonomy, and research on harvest and trade management plans. Although illegal collecting and harvesting is a known threat, orchids still suffer from black market trade including for collecting and products such as Salep and traditional medicines (Ghorbani et al. 2014; Hinsley et al. 2017a, b). With all orchids listed on the Convention on International Trade in Endangered Species (CITES) list, there are strict limits on orchid trade across countries; however, within many countries trade remains an issue (Hinsley et al. 2017a, b; Gale et al. 2019; Lawson et al. 2019).

Conservation priorities

With rapidly changing environments and limited conservation funding, it is important to focus conservation efforts on key priorities in targeted areas. Our study highlighted geographic patterns for these priorities and in some cases, priorities were broad based, such as species management which applied to many orchids around the world. This includes ex situ conservation, further developing genome resource banks and continuing work on propagation techniques. Protection and management of orchid habitat is another priority particularly for orchids threatened by biological resource use (illegal collection, harvesting and logging), development and agriculture globally which would also have a positive flow on effects for the entire ecosystems (Wan et al. 2014). However, large-scale conservation efforts involve a great deal of effort and planning including by governments and is currently not well addressed in key areas for orchids, such as Madagascar (Cribb and Hermans 2007; Harper et al. 2007).

Education and awareness are major priorities for orchid conservation including communication, especially for orchids threatened by human intrusion and disturbance including tourism and recreation (Swarts and Dixon 2009b; Wraith and Pickering 2017). This is important as much of on ground conservation is conducted and driven by community groups and societies both in terms of labour and funding (Light 2003). Increased awareness and education can be achieved by engaging local community groups and schools in conservation and propagation techniques (Dixon and Phillips 2007). In many cases, effective conservation measures can include simple actions such as signage to inform tourists how to minimise their impacts in protected areas, but also rely on researchers to better communicate their results with the general public (Wraith and Pickering 2017).

Law and policy was not seen as a high priority for orchid conservation based on the Red List data, but education and awareness were often listed. Due to the exploitation of orchids worldwide, it is important that orchid collectors and societies are aware of the importance of adhering to CITES regulations when exchanging orchid material (Hinsley et al. 2017a, b; Fay 2018; Gale et al. 2019). However, even with strict regulations, the illegal collection and trade of orchids remains prevalent across the globe (Wraith and Pickering 2018; Lawson et al. 2019). The effectiveness of the current CITES regulations and other protocols require both revision and stricter implementation to successful reduce the illegal orchid trade (Lawson et al. 2019). Orchids in Cypripedilinae had the largest number of threatened species with law and policy a priority, which was not surprising as Paphiopedilum orchids have a long history of illegal collecting (Thomas 2006; Ballantyne and Pickering 2012; Wraith and Pickering 2017). Interestingly law and policy were not listed as a priority for orchids in Madagascar, which has the largest number of threatened species. Livelihood, economic and other incentives were listed as the lowest priority for orchid conservation, except for orchids in East Asia including in China, Vietnam and India. This was also a priority for certain orchid tribes including Cypripedilinae and Cypripedieae and those orchids threatened by pollution.

Gaps in research and conservation

Based on our review of the current scope of research into orchid conservation and the priorities on IUCN Red List, there are some important gaps. This includes the need for more research on understanding and monitoring populations, trends and distributions for threatened species including assessing the impacts of climate change so we can better focus on ground conservation (Fig. 6). Due the vast diversity of orchids with most species relying on highly specific and complex interactions with other biota, future research could further focus on the ecology of threatened orchids including their interactions with fungi, pollinators, habitats and threats. We increasingly know about threats to orchids on a broad scale but understanding finer scale threats to specific species and how to mitigate them requires more research including links between species ecology and spatial distribution modelling (Fig. 6). For example, mapping fine scale distributions of threats could highlight appropriate areas for translocation and/or relocation of specific species. Three major gaps in conservation were highlighted by our study (Fig. 6). The first is protection and management of orchid species which can involve physical efforts such as caging populations or developing management plans in collaboration with local governments and land managers. The second involves protecting threatened orchid habitats and third is education, awareness and communication (Fig. 6).

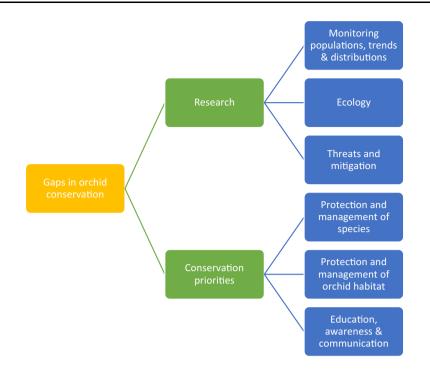


Fig. 6 A conceptual diagram highlighting gaps between research in orchid conservation and the research priorities for orchids on the IUCN Red List

Limitations

Important limitations to our knowledge about threats and priorities need to be considered. There are limitations when using academic literature to facilitate analyses due to social, economic and perceptions such as favoured taxa and biomes which can cause biases in spatial and temporal patterns (Pickering et al. 2018). In this study, we used data from a range of sources including the IUCN Red List which have limitations. As the IUCN Red List relies on data submitted by countries, there are important gaps. Data can often be over simplified, for example orchids listed in China have every conservation priority listed for each species and although it is possible that each species requires all priorities, this seems unlikely. Other limitations come from missing or outdated data. For instance, countries such as Australia have few orchids on the IUCN Red List, but many orchids listed as threatened on the national list (Wraith and Pickering 2018). It is important that countries accurately contribute to global listings such as the IUCN Red List and that the data are updated frequently as this will not only contribute to accurate assessments of global patterns of threats and threatened species but help to focus research and management priorities more broadly. Here we also used global species occurrence records from the Global Biodiversity Information Facility (GBIF 2019) which is an important resource for assessing global patterns in biodiversity and threats, but like many such resources has limitations. For example, these types of crowd-sourced databases often include inaccuracies in records such as missing or vague coordinates, low resolution location data, misidentified species and sampling bias (Hortal et al. 2007; Meyer 2016). These biases were reduced through an initial assessment of records and by visually assessing and removing points that were determined to be suspect.

As biodiversity is facing increasing diversity and severity of threats, most obviously from climate change, securing resources and funding for specific groups or species is both even more important, but also increasingly difficult. Although we highlighted where orchid conservation and research efforts should focus, it not realistic to assume that these can and will be achieved in a timely manner. Each of these priorities requires funding, governmental cooperation, community action and engagement and time, which for many species is quickly running out. Global collaboration and communication are crucial to conservation success particularly for orchids which include some of the most complex and rarest species on the planet.

CONCLUSIONS

Orchid conservation research has focused on taxonomy in the past and more recently on genetic diversity, mycorrhizal symbionts and propagation techniques, all of which are vital for successful orchid conservation. However, orchid conservation research should increasingly focus on population monitoring, species distribution and climate change impacts and adaptation, better understanding orchid ecology including habitat requirements and threat mitigation. Also, on ground orchid conservation should increasingly focus on protection and management of individual species as well as habitats, contributing to the survival of orchids and their communities. As orchid conservation often relies on the generosity of local governments, land managers, orchid societies and conservation action groups, education, awareness and communication between researchers and these communities remains critical.

Acknowledgements We thank Professor Charles Lawson for editing this manuscript. We also kindly thank the anonymous reviewers and editors for their comments which greatly improved the manuscript.

REFERENCES

- Ballantyne, M., and C. Pickering. 2012. Ecotourism as a threatening process for wild orchids. *Journal of Ecotourism* 11: 34–47.
- Brook, B.W., N.S. Sodhi, and C.J. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology & Evolution* 23: 453–460.
- Brundrett, M.C. 2019. A comprehensive study of orchid seed production relative to pollination traits, plant density and climate in an urban reserve in Western Australia. *Diversity* 11: 123.
- Case, M.A., H.T. Mlodozeniec, L.E. Wallace, and T.W. Weldy. 1998. Conservation genetics and taxonomic status of the rare Kentucky lady's slipper: *Cypripedium kentuckiense* Orchidaceae. *American Journal of Botany* 85: 1779–1786.
- Ceballos, G., P.R. Ehrlich, A.D. Barnosky, A. García, R.M. Pringle, and T.M. Palmer. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances* 1: e1400253.
- Ceballos, G., A. García, and P.R. Ehrlich. 2010. The sixth extinction crisis: Loss of animal populations and species. *Journal of Cosmology* 8: 31.
- Centre for Science and Technology Studies. 2019. VOSviewer. Version 1.6.11. https://www.vosviewer.com. Accessed 1 June 2019.
- Chamberlain, S., V. Barve, D. Mcglinn, D. Oldoni, P. Desmet, L. Geffert, and K. Ram. 2019. rgbif: Interface to the Global Biodiversity Information Facility API. R package version 1.3.0. https://CRAN.R-project.org/package=rgbif. Accessed 20 June 2019.
- Chung, M.Y., J.D. Nason, and M.G. Chung. 2004. Spatial genetic structure in populations of the terrestrial orchid *Cephalanthera longibracteata* Orchidaceae. *American Journal of Botany* 91: 52–57.
- Clarke, K.R., and R.N. Gorley. 2006. *PRIMER-E Version 6*. Plymouth: PRIMER-E.
- Cribb, P., and J. Hermans. 2007. The conservation of Madagascar's orchids. A model for an integrated conservation project. *Lankesteriana International Journal on Orchidology* 7: 255–261.
- Díaz, S., J. Settele, E. S. Brondizio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, et al. 2019. IPBES. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, IPBES secretariat, Bonn, Germany, 3–14.

- Dixon, K., and R.D. Phillips. 2007. The orchid conservation challenge. *Lankesteriana International Journal on Orchidology* 7: 11–12.
- Fay, M.F. 2018. Orchid conservation: How can we meet the challenges in the twenty-first century? *Botanical Studies* 59: 16.
- Forrest, A., M. Hollingsworth, P. Hollingsworth, C. Sydes, and R. Bateman. 2004. Population genetic structure in European populations of *Spiranthes romanzoffiana* set in the context of other genetic studies on orchids. *Heredity* 92: 218.
- Gale, S.W., P. Kumar, A. Hinsley, M.L. Cheuk, J. Gao, H. Liu, Z.-L. Liu, and S.J. Williams. 2019. Quantifying the trade in wildcollected ornamental orchids in South China: Diversity, volume and value gradients underscore the primacy of supply. *Biological Conservation* 238: 108204.
- GBIF. 2019. GBIF Home Page. https://www.gbif.org. Accessed 20 June 2019.
- Ghorbani, A., B. Gravendeel, F. Naghibi, and H. de Boer. 2014. Wild orchid tuber collection in Iran: A wake-up call for conservation. *Biodiveristy and Conservation* 23: 2749–2760.
- Hanski, I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio* 40: 248–255. https://doi.org/ 10.1007/s13280-011-0147-3.
- Harper, G.J., M.K. Steininger, C.J. Tucker, D. Juhn, and F. Hawkins. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34: 325–333.
- Hinsley, A., H.J. de Boer, M.F. Fay, S.W. Gale, L.M. Gardiner, R.S. Gunasekara, P. Kumar, S. Masters, et al. 2017a. A review of the trade in orchids and its implications for conservation. *Botanical Journal of the Linnean Society* 186: 435–455.
- Hinsley, A., A. Nuno, M. Ridout, F.A.S. John, and D.L. Roberts. 2017b. Estimating the extent of CITES noncompliance among traders and end-consumers; lessons from the global orchid trade. *Conservation Letters* 10: 602–609.
- Hortal, J., J.M. Lobo, and A. Jiménez-Valverde. 2007. Limitations of biodiversity databases: Case study on seed-plant diversity in Tenerife, Canary Islands. *Conservation Biology* 21: 853–863.
- IUCN. 2019. The IUCN Red List of Threatened Species. Version 2019-2. http://www.iucnredlist.org. Accessed 1 Mar 2019.
- Kull, T., M. Sammul, K. Kull, K. Lanno, K. Tali, B. Gruber, D. Schmeller, and K. Henle. 2008. Necessity and reality of monitoring threatened European vascular plants. *Biodiversity* and Conservation 17: 3383.
- Larsen, F.W., M.C. Londoño-Murcia, and W.R. Turner. 2011. Global priorities for conservation of threatened species, carbon storage, and freshwater services: Scope for synergy? *Conservation Letters* 4: 355–363.
- Lawson, C., J. Wraith, and C.M. Pickering. 2019. Regulating wild collected orchids? The CBD, Nagoya Protocol and CITES overlaps. *Environmental and Planning Law Journal* 36: 339–361.
- Light, M.H. 2003. Conservation through education. Lankesteriana International Journal on Orchidology 7: 125–126.
- Linde, C.C., T.W. May, R.D. Phillips, M. Ruibal, L.M. Smith, and R. Peakall. 2017. New species of Tulasnella associated with terrestrial orchids in Australia. *IMA Fungus* 8: 28.
- Liu, H., C. Feng, Y. Luo, B. Chen, Z. Wang, and H. Gu. 2010a. Potential challenges of climate change to orchid conservation in a wild orchid hotspot in southwestern China. *The Botanical Review* 76: 174–192.
- Liu, H., Y. Luo, and H. Liu. 2010b. Studies of mycorrhizal fungi of Chinese orchids and their role in orchid conservation in China— A review. *The Botanical Review* 76: 241–262.
- Martín-Martín, A., E. Orduna-Malea, M. Thelwall, and E.D. López-Cózar. 2018. Google Scholar, Web of Science, and Scopus: A systematic comparison of citations in 252 subject categories. *Journal of Informetrics* 12: 1160–1177.

- McCormick, M.K., and H. Jacquemyn. 2014. What constrains the distribution of orchid populations? *New Phytologist* 202: 392–400.
- McCormick, M.K., D. Lee Taylor, K. Juhaszova, R.K. Burnett Jr., D.F. Whigham, and J.P. O'Neill. 2012. Limitations on orchid recruitment: Not a simple picture. *Molecular Ecology* 21: 1511–1523.
- Meyer, C. 2016. Limitations in global information on species occurrences. *Frontiers of Biogeography* 8: e28195.
- Peakall, R., D. Ebert, J. Poldy, R.A. Barrow, W. Francke, C.C. Bower, and F.P. Schiestl. 2010. Pollinator specificity, floral odour chemistry and the phylogeny of Australian sexually deceptive Chiloglottis orchids: Implications for pollinator-driven speciation. *New Phytologist* 188: 437–450.
- Pickering, C., S.D. Rossi, A. Hernando, and A. Barros. 2018. Current knowledge and future research directions for the monitoring and management of visitors in recreational and protected areas. *Journal of Outdoor Recreation and Tourism* 21: 10–18.
- Phillips, R.D., R. Peakall, B.A. Retter, K. Montgomery, M.H.M. Menz, B.J. Davis, C. Hayes, G.R. Brown, et al. 2015. Pollinator rarity as a threat to a plant with a specialized pollination system. *Botanical Journal of the Linnean Society* 179: 511–525.
- Pillon, Y., F. Qamaruz-Zaman, M.F. Fay, F. Hendoux, and Y. Piquot. 2007. Genetic diversity and ecological differentiation in the endangered fen orchid *Liparis loeselii*. *Conservation Genetics* 8: 177.
- QGIS Development Team. 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project 3.8.6. http://qgis.osgeo.org. Accessed 1 Aug 2019.
- R Core Team. 2019. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Reiter, N., A.C. Lawrie, and C.C. Linde. 2018. Matching symbiotic associations of an endangered orchid to habitat to improve conservation outcomes. *Annals of Botany* 122: 947–959.
- Reiter, N., K. Vlcek, N. O'Brien, M. Gibson, D. Pitts, G.R. Brown, C.C. Bower, and R.D. Phillips. 2017. Pollinator rarity limits reintroduction sites in an endangered sexually deceptive orchid *Caladenia hastata*: Implications for plants with specialized pollination systems. *Botanical Journal of the Linnean Society* 184: 122–136.
- Reiter, N., J. Whitfield, G. Pollard, W. Bedggood, M. Argall, K. Dixon, B. Davis, and N. Swarts. 2016. Orchid re-introductions: An evaluation of success and ecological considerations using key comparative studies from Australia. *Plant Ecology* 217: 81–95.
- RStudioTeam. 2016. *RStudio: Integrated Development for R*. Boston: RStudio Inc.
- Sayers, E.W., T. Barrett, D.A. Benson, E. Bolton, S.H. Bryant, K. Canese, V. Chetvernin, D.M. Church, et al. 2009. Database resources of the national center for biotechnology information. *Nucleic Acids Research* 38: D5–D16.
- Seaton, P., J.P. Kendon, H.W. Pritchard, D.M. Puspitaningtyas, and T.R. Marks. 2013. Orchid conservation: The next ten years. *Lankesteriana International Journal on Orchidology* 13: 93–101.
- Seaton, P.T., H. Hu, H. Perner, and H.W. Pritchard. 2010. Ex situ conservation of orchids in a warming world. *The Botanical Review* 76: 193–203.
- Simmons, L., M.T. Mathieson, R.W. Lamont, and A. Shapcott. 2018. Genetic diversity of endangered orchid *Phaius australis* across a fragmented Australian landscape. *Conservation Genetics* 19: 451–465.
- Stork, N.E. 2010. Re-assessing current extinction rates. *Biodiversity* and Conservation 19: 357–371.
- Swarts, N.D., and K.W. Dixon. 2009a. Terrestrial orchid conservation in the age of extinction. *Annals of Botany* 104: 543–556.

- Swarts, N.D., and K.W. Dixon. 2009b. Perspectives on orchid conservation in botanic gardens. *Trends in Plant Science* 14: 590–598.
- Swarts, N.D., E.A. Sinclair, S.L. Krauss, and K.W. Dixon. 2009. Genetic diversity in fragmented populations of the critically endangered spider orchid *Caladenia huegelii*: Implications for conservation. *Conservation Genetics* 10: 1199–1208.
- Thomas, B.A. 2006. Slippers, thieves and smugglers—Dealing with the illegal international trade in orchids. *Environmental Law Review* 8: 85–92.
- Urban, M.C. 2015. Accelerating extinction risk from climate change. Science 348: 571–573.
- Valiente-Banuet, A., M.A. Aizen, J.M. Alcántara, J. Arroyo, A. Cocucci, M. Galetti, M.B. García, D. García, et al. 2015. Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology* 29: 299–307.
- Wan, J., C. Wang, S. Han, and J. Yu. 2014. Planning the priority protected areas of endangered orchid species in northeastern China. *Biodiversity and Conservation* 23: 1395–1409.
- Wraith, J., and C. Pickering. 2018. Quantifying anthropogenic threats to orchids using the IUCN Red List. *Ambio* 47: 307–317. https:// doi.org/10.1007/s13280-017-0964-0.
- Wraith, J., and C. Pickering. 2017. Tourism and recreation a global threat to orchids. *Biodiversity and Conservation* 26: 3407–3420.
- Wraith, J., and C. Pickering. 2019. A continental scale analysis of threats to orchids. *Biological Conservation* 234: 7–17.
- Yeung, E.C. 2017. A perspective on orchid seed and protocorm development. *Botanical Studies* 58: 33.
- Zuguang, G., L. Gu, R. Eils, M. Schlesner, and B. Brors. 2014. Circlize implements and enhances circular visualization in R. *Bioinformatics* 30: 2811–2812.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

AUTHOR BIOGRAPHIES

Jenna Wraith (\boxtimes) is a doctoral candidate in the Environmental Futures Research Institute and in the School of Environment and Science at Griffith University, Australia. Her research interests include conservation biology, global biodiversity, threatening processes, species distributions and climate change.

Address: Griffith School of Environment, Environmental Futures Research Institute, Griffith University, Parklands Drive, Southport, Gold Coast, QLD 4222, Australia.

e-mail: jenna.wraith@griffithuni.edu.au

Patrick Norman is a doctoral candidate in the Environmental Futures Research Institute and in the School of Environment and Science at Griffith University, Australia. His research interests include volunteered geographic information, remote sensing, spatial analyses, botany and ecology.

Address: Griffith School of Environment, Environmental Futures Research Institute, Griffith University, Parklands Drive, Southport, Gold Coast, QLD 4222, Australia.

e-mail: Patrick.norman@griffithuni.edu.au

Catherine Pickering is a Professor in the Environmental Futures Research Institute and in the School of Environment and Science at Griffith University, Australia. Her research interest includes botany, ecology, park management, climate change and research methodology including systematic quantitative literature reviews.

Address: Griffith School of Environment, Environmental Futures Research Institute, Griffith University, Parklands Drive, Southport, Gold Coast, QLD 4222, Australia.

e-mail: c.pickering@griffith.edu.au