

Review Paper

Conservation of carnivorous plants in the age of extinction

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ABSTRACT

Carnivorous plants (CPs)—those possessing specific strategies to attract, capture and kill animal prey and obtain nutrition through the absorption of their biomass—are harbingers of anthropogenic degradation and destruction of ecosystems. CPs exhibit highly specialised and often very sensitive ecologies, being generally restricted to nutrient-impooverished habitats where carnivory offers a competitive advantage. As such, they are often the first species to disappear following habitat degradation, land use change, and alteration to natural ecological processes, and are at significant risk from processes such as eutrophication and weed invasion, and even poorly-understood impacts such as airborne nitrogen inputs. Many of the world's 860 species of CPs are found in wetland habitats, which represent some of the most cleared and heavily degraded ecosystems on Earth. Global diversity hotspots for CPs are likewise located in some of the most heavily cleared and disturbed areas of the planet—southwestern Western Australia, Southeast Asia, Mediterranean Europe, central eastern Brazil, and the southeastern United States—placing their conservation at odds with human developmental interests. Many carnivorous plant species exhibit extreme range-restriction and are wholly localised to specific geological formations, microhabitats or elevations, with nowhere to move to in the face of environmental change, such as a warming, drying climate. We provide the first systematic examination of the conservation status and threats to all CPs globally, compiling full or partial assessments of conservation status category for 860 species from 18 genera, and provide ten recommendations towards better conservation and management of this iconic group. A total of 69 species were assessed as Critically Endangered (8% of all species), 47 as Endangered (6%), 104 as Vulnerable (12%), and 23 as Near Threatened (3%). Slightly over 60% of CPs (521 species) were assessed as Least Concern. At least 89 species are known from only a single location based on current knowledge. Data on threatening processes were available for 790 species, with the most common threatening processes including *Agriculture and Aquaculture* (impacting 170 species), *Natural Systems Modifications* (168 species), *Climate Change and Severe Weather* (158 species), *Energy Production and Mining* (127 species), *Human Intrusions and Disturbance* (126 species), and *Biological Resource Use* (98 species). Almost a quarter of all species were impacted upon by three or more threatening processes. The most significant threats placing species at imminent risk of extinction include the continuing clearing of natural habitat for urban and agricultural development and the illegal collection of individuals from the wild for horticultural trade.

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The complex and specialised ecological requirements of CPs, together with the multifaceted threats they face, make conservation difficult and repatriation even to restored areas challenging. As the number of vulnerable, endangered and extinct carnivorous plant species continues to grow, despite significant conservation efforts in many regions and greater awareness of their ecological requirements, it is clear that a paradigm shift is required in our approach to the preservation of this unique group of plants in order to achieve long-term conservation successes.

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1. Introduction

Carnivorous plants (CPs) are an iconic and captivating group of plants. While most historic scientific interest in this group has focussed on their biology, ecology and nutrient acquisition strategies, CPs and other highly ecologically specialised plants are increasingly recognised as being at risk from a range of anthropogenic influences in a changing world (e.g., Swarts and Dixon, 2009; Jennings and Rohr, 2011; Clarke et al., 2018; Cross, 2019). A review by Jennings and Rohr (2011) classified the threatening processes affecting CPs into eleven generalised categories, and found that the most common included 'habitat loss from agriculture', 'the collection of wild plants', 'pollution', and 'natural systems modifications'. However, at the time of their review only around 600 species of CPs were described from 17 genera, and information on threatening processes were available for only 48 species (Jennings and Rohr, 2011). In the ensuing decade, there has been a significant increase in the number of species for which up-to-date information exists on threatening processes, while a large number of new species of CPs have been discovered and described in papers with integral threat assessments, particularly from biodiverse regions such as northern and southwestern Australia (e.g., Jobson, 2013; Jobson and Baleerio, 2015; Robinson et al., 2018), Borneo, Malaysia and the Philippines (e.g., Lagunday et al., 2017; Robinson et al., 2019a, 2019b; Golos et al., 2020), and Brazil (e.g., Fleischmann et al., 2011, 2017; Souza and Bove, 2011; Carvalho and Queiroz, 2014; Rivadavia et al., 2013, 2014; Gonella et al., 2014, 2015; Gonella and Baleeiro, 2018; Scatigna et al., 2015, Scatigna et al., 2017). As of January 2020, exactly 860 species of CPs had been described from 18 genera (Ellison and Adamec, 2018, updated since by the authors of the present work).

Recent studies have highlighted significant conservation concerns for an increasing number of iconic CP species around the world: the cosmopolitan *Aldrovanda vesiculosa* (Cross, 2012a, 2012b; Cross et al., 2015, 2016; Adamec, 2018; Cross and Adamec, 2020); *Byblis gigantea* and *Cephalotus follicularis* from southwestern Western Australia (Cross et al., 2013; Cross et al., 2018b, 2019; Bradshaw et al., 2018; Just et al., 2019); *Drosera peltata* from the southern Mediterranean (Paniw et al., 2015; Cross et al., 2017; Gómez-González et al., 2018; Skates et al., 2019); *Triphyophyllum peltatum* from western Africa (Cross et al., 2018b); many *Nepenthes* from southeast Asia (Clarke et al., 2018; Robinson et al., 2019a, 2019b); almost all species of *Sarracenia* from North America (U.S. Fish and Wildlife Service 1991; Schnell, 2002; Koopman and Carstens, 2010; Jennings and Rohr, 2011); and a number of *Drosera* species from South America, South Africa and Australia (de Stefano and dos Santos Silva, 2001; Gonella et al., 2016; Robinson et al., 2017; Clarke et al., 2018; Fleischmann et al., 2018).

Climatic modelling and niche predictions under predicted climate scenarios suggest many CP species around the world face an uncertain and potentially challenging future, with nearly 70% of modeled species exhibiting negative median bioclimatic velocity and several species predicted to experience a 100% loss of potential range area by 2050 (Fitzpatrick and Ellison, 2018). It appears that increasing numbers of CPs, from almost all regions in which they occur, face growing pressure from a broadening diversity of threatening processes including increasing habitat loss which is a primary global driver of biodiversity erosion (e.g., Dobson et al., 2006; Betts et al., 2017; Thompson et al., 2017; Staude et al., 2018). The scale of habitat loss in regions harbouring high CP biodiversity ranges from fine-scale selective removal of species such as hardwood trees through forestry and illegal logging in countries such as Indonesia and those of West Africa (Jepson et al., 2001; Nellemann, 2007; Arcilla et al., 2015), to the landscape-scale replacement of natural vegetation with production monocultures such as *Eucalyptus* plantations in southeast Brazil (Ribas et al., 2016), and palm oil or cereal crops in southeast Asia and Western Australia (Nellemann, 2007; Fitzherbert et al., 2008; Bradshaw, 2012; Lee et al., 2014). Although the spatial scale and regional intensity of habitat loss is dependent upon its underlying drivers and mechanisms (De Chazal and Rounsevell, 2009; de Castro Solar et al., 2016), the ecological impacts of even small-scale disturbances on species and ecosystems can be profound (Hobbs and Huenneke, 1992; Langhans et al., 2010), particularly where the cumulative impacts of multiple activities begin to reduce habitat connectivity and the maintenance of natural ecological processes such as hydrology, fire, pollination, and dispersal (Theobald et al., 1997; Vanbergen and Initiative, 2013; Auffret et al., 2017). Some CP species are being recognised as at risk of extinction from threats such as habitat destruction, poaching and/or climatic change even as they are being discovered, including the iconic giants *Nepenthes attenboroughii* (Robinson et al., 2009) and *Drosera magnifica* (Gonella et al., 2015).

In recognition of the growing need to examine and maintain the currency of conservation status category for this group, the Carnivorous Plant Specialist Group (CPSG; <http://www.iucn-cpsg.org/>) of the International Union for the Conservation of Nature (IUCN) Species Survival Commission was established and has undertaken numerous conservation status assessments of CPs for the IUCN Red List of Threatened Species. However, while Clarke et al. (2018) overviewed the conservation status category of CPs following the assessment of ca. 300 previously unassessed species by the CPSG in 2016, no systematic global

review of the conservation status category and threatening processes impacting CPs has been conducted since the work of Jennings and Rohr (2011).

This study provides a systematic reexamination of the conservation status and threats to CPs globally, greatly improving the species coverage achieved by Jennings and Rohr (2011) and determining whether regional and global threats to this iconic plant group have become better resolved in the intervening decade. We aimed to i) provide an assessment of conservation status category (IUCN Red List category) for all currently-described CP species; ii) determine which threatening processes presented the greatest impacts to CPs globally; iii) determine whether putative micro-endemics (i.e., species known from only from a limited geographical range, sometimes just one locality) or species impacted upon by multiple threatening processes were significantly more likely to be assessed at greater risk of extinction (i.e., a higher conservation status category); and iv) identify regions harbouring the greatest numbers of threatened CPs to evaluate the highest conservation responsibilities on a global scale and assist and prioritising management efforts. CP species often exhibit highly complex biological mutualisms, sometimes providing crucial habitat or resources for other organisms (e.g., Grafe et al., 2011; Bazile et al., 2012; Cross et al., 2018b, 2019), and some ecologically sensitive species have been described as harbingers of ecosystem decline and habitat degradation (e.g., Cross, 2012a). Jennings and Rohr (2011) noted that the appropriate conservation and management of CPs was “likely to help maintain the important ecosystem services they provide and prevent secondary extinctions of specialist species that rely on them”, and that their loss from ecosystems could cause cascading secondary effects including extirpations and extinctions. As anthropogenic degrading factors continue to deplete taxonomic, genetic and functional diversity in ecosystems worldwide (Naeem et al., 2012), the conservation of highly specialised or range-restricted species occupying small or highly-specific ecological niches becomes ever more challenging (Swarts and Dixon, 2009). The prioritisation, financing and establishment of appropriate conservation and management activities requires accurate and contemporary information.

2. Methods

Following the methods of Jennings and Rohr (2011), entries for all carnivorous plants currently assessed in the IUCN Red List database (www.iucnredlist.org) were extracted on 20 January 2020. The National Red List database (www.nationalredlist.org) was also searched on 20 January 2020 for all carnivorous plant genera (published to that date): *Aldrovanda* [one species], *Brocchinia* [only the two carnivorous species were considered], *Byblis* [eight species], *Catopsis* [one species], *Cephalotus* [one species], *Darlingtonia* [one species], *Dionaea* [one species], *Drosera* [248 species], *Drosophyllum* [one species], *Genlisea* [30 species], *Heliophora* [23 species], *Nepenthes* [169 species], *Philcoxia* [seven species], *Pinguicula* [105 species], *Roridula* [two species], *Sarracenia* [11 species], *Triphyophyllum* [one species], and *Utricularia* [248 species]. “Paracarnivorous” species were excluded from analyses; for example, Nishi et al. (2013) propose carnivory in *Paepalanthus bromelioides* (Eriocaulaceae), but the absorptive capacity of its leaf trichomes remains unclear (Cross et al., 2018b) and thus the species is not generally regarded as carnivorous. To supplement these lists with species for which information on conservation status and threatening processes were published but not yet assessed by the IUCN, we conducted a search using Web of Knowledge, Google Scholar and Scopus to identify relevant peer-reviewed literature using the keywords ‘carnivorous plants’, ‘conservation’, ‘threats’, ‘threatening’ and each carnivorous plant genus name. Published conservation statuses, mainly from species descriptions, were included only where species had been assessed recently (2000 onwards) using the IUCN framework and principles. Where adequate data on distribution and threats were available in the published literature but no conservation status yet proposed, we used these data to assess species against the current IUCN criteria version (3.1) to provide each with an indicative conservation status (the authors having combined experience in assessing over 500 species for the IUCN Red List) under the standard IUCN categories (IUCN, 2012), namely Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), Extinct (EX) and Data Deficient (DD). Area of Occurrence (AOO) and Extent of Occurrence (EOO) values were extracted from IUCN assessments or published literature, or were generated from GeoCAT (<http://geocat.kew.org/>) consistent with IUCN methodology for species where sufficient distributional data were available, using published distribution data and quality-controlled Global Biodiversity Information Facility (GBIF.org, 2020), Atlas of Living Australia (ALA) and iNaturalist.org records. Only records from 1970 onwards were used, and all records were checked to ensure instances of cultivated, misidentified and erroneous locations were excluded. For consistency, and to facilitate analyses, we present data from global assessments of each species only; it should be noted that the conservation status of some species examined here may vary among specific regions or jurisdictions.

All documented threats to each species were classified following the unified scheme proposed by Salafsky et al. (2008), as adopted by the current IUCN criteria version (3.1) and by Jennings and Rohr (2011). This scheme comprises three hierarchical levels of threats increasing in specificity with each level, beginning with 11 first level categories: (1) *Residential and Commercial Development*, (2) *Agriculture and Aquaculture*, (3) *Energy Production and Mining*, (4) *Transportation and Service Corridors*, (5) *Biological Resource Use*, (6) *Human Intrusions and Disturbance*, (7) *Natural Systems Modifications*, (8) *Invasive and Other Problematic Species and Genes*, (9) *Pollution*, (10) *Geological Events*, and (11) *Climate Change and Severe Weather*. While second and third level categories further defining threatening processes are sometimes presented in conservation assessments (e.g., Cross, 2020b; Fleischmann et al., 2011, 2017, 2020; Gonella et al., 2016; Robinson et al., 2009, 2018, 2019b), for the purposes of consistency and statistical analyses we present only first level threatening process categories for species in this study. Data on threatening processes for species assessed by the IUCN were updated where the published literature provided more contemporary evidence.

For speciose genera (defined for the purposes of analyses as genera containing >5 species *sensu* Jennings and Rohr, 2011, and as the test is sensitive to small frequencies and can lead to erroneous conclusions when run with five or fewer samples), a chi-square test of homogeneity was conducted between genera and number of threatened species (with species pooled into groups of 'Data Deficient', 'Least Concern', and 'Threatened' to ensure all expected cell frequencies were >5). Chi-square tests of homogeneity were also conducted between genera and number of species impacted upon by each of the 11 first level threatening process categories (for all species with information available on threatening processes), but could only be run for the four largest genera (*Drosera*, *Utricularia*, *Nepenthes* and *Pinguicula*) to ensure all expected cell frequencies were >5. To determine whether a relationship existed between distribution and conservation status, we ran two-tailed bivariate correlation with Pearson correlation coefficients individually between conservation status (transformed to an ordinal variable from 1 [LC] to 5 [CR] for each species) and AOO, EOO and EOO/AOO. To determine whether any factors significantly predicted increasing conservation status category (as an indicator of increased level of risk of extinction, increasing from LC to CR), multiple linear regression models were fitted to examine the effect of *Micro-endemism* (being known from only a single location), *Number of Threats* (the total number of threatening process categories impacting upon the species), and whether the species was impacted upon by each of the 11 first level threatening process categories, on conservation status (transformed to an ordinal variable from 1 [LC] to 5 [CR] for each species). Stepwise model reduction was completed through minimising the Akaike's Information Criterion (AIC). Species classified as DD were excluded from regression analyses.

To visualise the relationship among threatening process categories, among carnivorous plant species, and between threatening process categories and species, a principal coordinate analysis (PCoA) based on Jaccard's distance was conducted using the software package CANOCO 5 (Biometris, Wageningen, NL) *sensu* Jennings and Rohr (2011). Variables included the 11 first level threatening process categories, and the PCoA analysis included a species × threatening process matrix (790 species × 11 threatening process categories), with only species for which data were available on threatening processes included in the matrix.

3. Results

3.1. Conservation status

Full or partial assessments of conservation status category were entered or compiled for all 860 species of carnivorous plants from 18 genera that had been described by 20 January 2020 (Table 1, Appendix S1). These comprised 495 species assessed by the IUCN (57.6% of species), 32 species assessed in National Red Lists but not by the IUCN (3.7%), 75 species assessments derived from the recent published literature (8.7%), and 258 species (30%) assessed by the authors on the basis of available information on distribution and threats. Over 90% of all assessments were conducted in the last decade. CR species were recorded from 17 countries, although Brazil, Indonesia and the Philippines together harboured over half of all CR species (Table 2).

Approximately a quarter of the 860 currently described species of CPs assessed were found to be at risk of extinction, with 8.0% of species assessed as CR, 5.5% as EN, 12.1% as VU and 2.7% as NT (Table 1). A further 11.2% were assessed as DD, indicating insufficient information was available on their distribution and threatening processes to confidently allocate them to any category from LC to CR (Table 1). Approximately 60% of species were assessed as LC (Fig. 1). There was a statistically significant association between genus and number of threatened species, $\chi^2(10) = 129.3$, Cramer's V = 0.280, $P < 0.001$.

Table 1

Numbers of species assessed in each conservation status category under the IUCN Red List criteria for all carnivorous plant genera.

Genus	CR	EN	VU	NT	LC	DD	Genus total
<i>Aldrovanda</i>	—	1	—	—	—	—	1
<i>Brocchinia</i>	—	—	—	—	2	—	2
<i>Byblis</i>	1	—	2	—	5	—	8
<i>Catopsis</i>	—	—	—	—	1	—	1
<i>Cephalotus</i>	—	—	1	—	—	—	1
<i>Darlingtonia</i>	—	—	—	—	1	—	1
<i>Dionaea</i>	—	—	1	—	—	—	1
<i>Drosera</i>	9	12	28	8	184	7	248
<i>Drosophyllum</i>	—	—	—	1	—	—	1
<i>Genlisea</i>	3	2	3	3	15	4	30
<i>Heliamphora</i>	—	—	6	—	13	4	23
<i>Nepenthes</i>	30	17	21	3	77	21	169
<i>Philcoxia</i>	6	1	—	—	—	—	7
<i>Pinguicula</i>	15	4	31	3	33	19	105
<i>Roridula</i>	—	—	2	—	—	—	2
<i>Sarracenia</i>	1	2	1	2	4	1	11
<i>Triphyophyllum</i>	—	—	—	—	—	1	1
<i>Utricularia</i>	4	8	8	3	186	39	248
Grand total	69	47	104	23	521	96	860

Species facing multiple threats and putative micro-endemics (i.e., species known from only one location) were significantly more likely to be assessed at greater risk of extinction (i.e., a higher conservation status category). Regression analyses statistically significantly predicted increasing conservation status category (overall model $F(8) = 83.854$, $P < 0.001$), with increasing conservation status category best predicted by a model including the predictors *Micro-endemism* (Beta = -0.401 , $t = -14.402$, $P < 0.001$), *Number of Threats* (Beta = 0.517 , $t = 7.636$, $P < 0.001$), *Residential and Commercial Development* (Beta = -0.156 , $t = -4.239$, $P < 0.001$), *Transportation and Service Corridors* (Beta = -0.069 , $t = -2.096$, $P = 0.036$), *Biological Resource Use* (Beta = -0.178 , $t = 5.701$, $P < 0.001$), *Human Intrusions and Disturbance* (Beta = 0.090 , $t = 2.190$, $P = 0.029$), *Pollution* (Beta = -0.176 , $t = -4.775$, $P < 0.001$) and *Geological Events* (Beta = -0.104 , $t = -3.743$, $P < 0.001$).

3.2. Area and extent of occurrence

A total of 89 species were known from only a single location based on current knowledge (putative micro-endemics, ca. 10% of all species), with insufficient information available to elucidate the distribution of a further 21 species. Data on AOO and EOO were available for 629 species (73% of species assessed) and 625 species (75%), respectively, while EOO/AOO could be calculated for 622 species (Appendix S1). AOO for all species ranged from 4 to 177910 km², and was strongly positively correlated with EOO ($R^2 = 0.758$, $P < 0.001$), which ranged from 4 to 277591043 km². With DD species excluded from analyses, AOO ($R^2 = -0.042$, $P = 0.301$), EOO ($R^2 = -0.084$, $P = 0.037$) and EOO/AOO ($R^2 = -0.084$, $P = 0.041$) all negatively correlated with increasing conservation status category (Table 3).

3.3. Threatening processes

Data on threatening processes were available for 790 species (92% of species assessed; Table 4), with species being affected by up to nine of the 11 high-level threatening process categories. Almost a quarter of species for which threats data were available were impacted upon by three or more threatening process categories (Appendix S1). The most common threatening processes identified for CP species included *Agriculture and Aquaculture* (170 species), *Natural Systems Modifications* (168 species), *Climate Change and Severe Weather* (158 species), *Energy Production and Mining* (127 species), *Human Intrusions and Disturbance* (126 species), and *Biological Resource Use* (98 species). The least common threatening process was *Geological Events* (listed only for five species of *Nepenthes*). Many of the significant threatening processes identified impact entire populations with immediate effect, and represent rapid and often irreversible changes to ecosystems or ecological functioning.

Agriculture and Aquaculture (most commonly relating to land clearing for broadacre agriculture or illegal logging activities), *Natural Systems Modifications* (most commonly being alterations to natural hydrological and fire regimes) and *Climate Change and Severe Weather* were ubiquitous threatening processes affecting species (or more specifically, their habitats) from almost every CP genus (Table 4). Among the four most speciose genera there was a strong statistically significant association between genus and number of species impacted upon by *Agriculture and Aquaculture* ($\chi^2(3) = 18.8$, $P < 0.001$; Cramer's $V = 0.164$, $P < 0.001$), *Natural Systems Modifications* ($\chi^2(3) = 62.8$, $P < 0.001$; Cramer's $V = 0.300$, $P < 0.001$) and *Climate Change and Severe Weather* ($\chi^2(3) = 95.3$, $P < 0.001$; Cramer's $V = 0.369$, $P < 0.001$), driven primarily in all cases by disproportionately high representation of these threats among species of *Drosera* and *Pinguicula*.

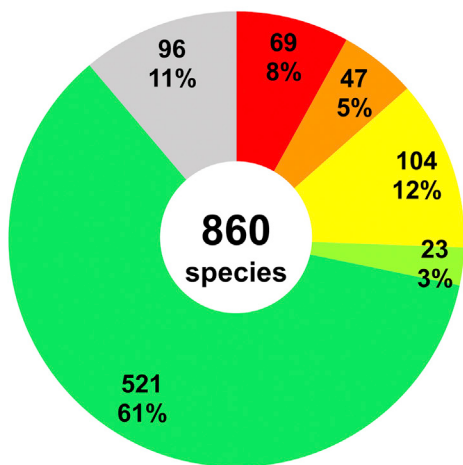
The impact of *Energy Production and Mining* was most commonly reported among speciose genera (those containing at least five species), particularly for *Philcoxia* (100% of species), *Genlisea* (63% of species) and *Pinguicula* (28% of species), while *Human Intrusions and Disturbance* most commonly affected *Philcoxia* (86% of species), *Genlisea* (47% of species) and *Pinguicula*.

Table 2

List of countries harbouring highest numbers of threatened carnivorous plant species (i.e. assessed CR, EN, or VU), ranked by number of CR species.

Country	CR	EN	VU	Total
Brazil	13	10	5	28
Indonesia	12	9	5	26
Philippines	10	3	9	22
Cuba	7	0	1	8
Thailand	5	0	0	5
Australia	4	4	22	30
Malaysia	4	3	6	13
Italy	3	1	1	5
Mexico	2	1	20	23
Cambodia	2	0	0	2
South Africa	1	2	9	12
USA	1	3	4	8
Venezuela	1	0	6	7
Czech Republic	1	0	1	2
Bolivia	1	0	0	1
DR Congo	1	0	0	1
Dominican Republic	1	0	0	1

All carnivorous plant genera



■ Critically Endangered ■ Near Threatened
■ Endangered ■ Least Concern
■ Vulnerable ■ Data Deficient

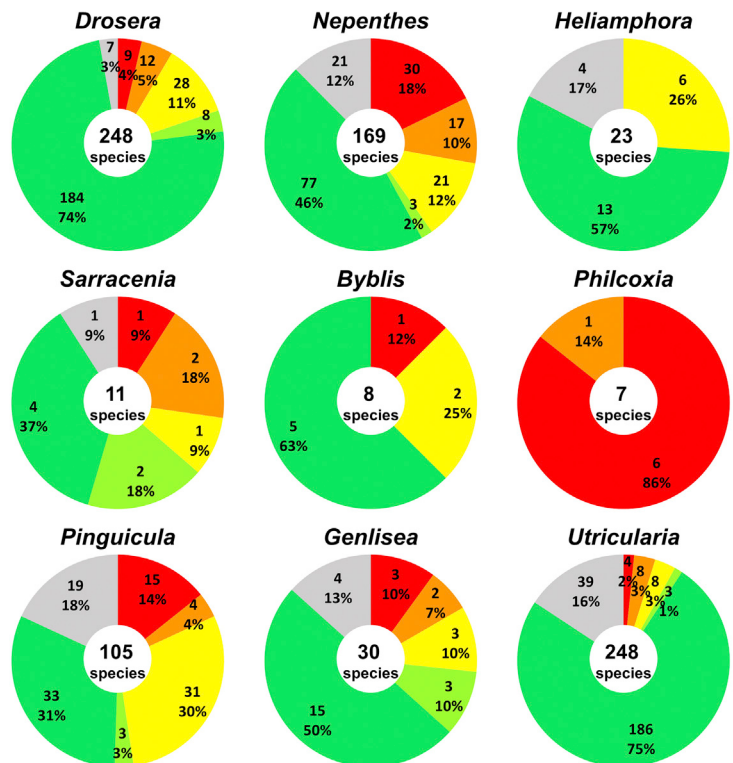


Fig. 1. Number of species and percentage proportion of all carnivorous plant species in each conservation status assessed under the IUCN Red List criteria, and number of species and percentage proportion assessed in each conservation status for the most speciose genera (genera containing >5 species), with genera arranged by phylogenetic affinity. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Mean $\pm$ s.e. for Area of Occurrence (AOO) and Extent of Occurrence (EOO), as well as EOO/AOO, of carnivorous plants assessed under the IUCN Red List criteria. EOO/AOO is an index of habitat occupancy, calculated by dividing total potential habitat (EOO, acknowledging that EOO often encompasses unsuitable habitat) by theoretical occupied habitat (AOO, acknowledging that populations of many species are much smaller than the 4 km² grid squares employed by the IUCN).

	AOO		EOO		EOO/AOO	
	Mean(km ²)	n	mean(km ²)	n	mean	n
Least Concern	842 $\pm$ 423.2	443	4137240 $\pm$ 804282.6	459	9893 $\pm$ 1147.2	442
Near Threatened	220 $\pm$ 169.4	13	13915 $\pm$ 11098.6	12	206 $\pm$ 144.5	12
Vulnerable	63 $\pm$ 145.6	70	10182 $\pm$ 4881.0	72	223 $\pm$ 118.1	66
Endangered	60 $\pm$ 17.7	30	16788 $\pm$ 13569.8 ^a	32	966 $\pm$ 847.4 ^a	32
Critically Endangered	9 $\pm$ 1.4	41	16 $\pm$ 4.6	40	1.4 $\pm$ 0.3	40
Data Deficient	11 $\pm$ 1.5	30	32125 $\pm$ 21666.5	30	2148 $\pm$ 1752.6	30

^a Excluding the cosmopolitan EN species *Aldrovanda vesiculosa*, which has an EOO of >114,000,000 km²; when this outlier was included the mean EOO for group 'Endangered' was 3586039 $\pm$ 3565275.3 km² and EOO/AOO was 15566 $\pm$ 14623.1.

(36% of species). Among the four most speciose genera there was a strong statistically significant association between genus and number of species impacted upon by *Energy Production and Mining* ($\chi^2(3)=47.5$, $P<0.001$; Cramer's $V=0.260$, $P<0.001$), driven primarily by disproportionately higher representation of this threat in species of *Pinguicula* and *Drosera*.

With almost one-third of all CPs threatened by *Residential and Commercial Development*, *Agriculture and Aquaculture*, or *Energy Production and Mining* (240 species), including 53% of CR, 57% of EN, 50% of VU, and 68% of NT species (Appendix S1), habitat loss and land use change clearly represents the most significant global threat to CPs. Given the average AOO for CR and EN species threatened by *Residential and Commercial Development*, *Agriculture and Aquaculture*, or *Energy Production and Mining* was only 10 and 76 km², respectively, with at least 17 of these CR species known from only one or two populations, the impacts of even small-scale disturbances are likely profound.

Over 10% of all species were threatened by *Biological Resource Use*, identified in most cases as the poaching of plants for illegal trade but also rarely for pharmaceutical/medical use (some species of *Drosera* and *Triphyophyllum peltatum*). Instances of *Biological Resource Use* as a threatening process was highest for species of *Sarracenia* (100% of species), *Nepenthes* (27% of

Table 4

Number of species from each carnivorous plant genus in each of 11 high-level threatening process categories. Many species are impacted by multiple threats, and are thus represented in multiple threat category columns. 1- Residential and Commercial Development. 2- Agriculture and Aquaculture. 3- Energy Production and Mining. 4- Transportation and Service Corridors. 5- Biological Resource Use. 6- Human Intrusions and Disturbance. 7- Natural Systems Modifications. 8- Invasive and Other Problematic Species and Genes. 9- Pollution. 10- Geological Events. 11- Climate Change and Severe Weather.

Genus (number of species)	1	2	3	4	5	6	7	8	9	10	11
<i>Aldrovanda</i> (1)	1	1	—	—	—	—	1	—	1	—	1
<i>Brocchinia</i> (2)	—	2	2	—	—	2	—	—	—	—	2
<i>Byblis</i> (8)	1	2	1	—	—	—	8	—	—	—	1
<i>Catopsis</i> (1)	—	—	—	—	—	—	—	—	—	—	—
<i>Cephalotus</i> (1)	1	1	—	—	1	—	1	—	—	—	1
<i>Darlingtonia</i> (1)	—	—	—	—	—	—	1	—	1	—	—
<i>Dionaea</i> (1)	1	1	—	1	1	1	1	—	1	—	1
<i>Drosera</i> (248)	30	59	49	15	10	44	78	45	23	—	65
<i>Drosophyllum</i> (1)	1	1	—	—	—	—	1	1	—	—	—
<i>Genlisea</i> (30)	7	19	19	17	—	14	5	3	23	—	27
<i>Heliamphora</i> (23)	—	—	—	—	1	2	2	1	1	—	—
<i>Nepenthes</i> (169)	3	24	10	6	45	4	8	—	1	5	1
<i>Philcoxia</i> (7)	—	5	7	7	—	6	—	—	—	—	7
<i>Pinguicula</i> (105)	7	22	29	13	24	38	32	8	11	—	39
<i>Roridula</i> (2)	—	1	1	—	2	2	2	—	1	—	1
<i>Sarracenia</i> (11)	11	11	—	—	11	—	11	11	11	—	3
<i>Triphyophyllum</i> (1)	—	1	1	1	1	1	—	—	—	—	—
<i>Utricularia</i> (248)	12	20	8	2	2	12	18	7	7	5	12
Total (860)	75	170	127	62	98	126	169	76	81	10	161

species) and *Pinguicula* (22% of species), and was considered a major threat to species from monospecific genera including *Cephalotus follicularis*, *Dionaea muscipula* and *Triphyophyllum peltatum*. Among the four most speciose genera there was a strong statistically significant association between genus and number of species impacted upon by *Biological Resource Use* ($\chi^2(3) = 124.5$, $P < 0.001$; Cramer's $V = 0.422$, $P < 0.001$), predominantly due to the number of *Nepenthes* species affected by this threat (45) being three times higher than statistically expected (14.5).

Among the four most speciose genera, statistically significant associations were also evident between genus and *Residential and Commercial Development* ($\chi^2(3) = 13.8$, $P = 0.003$; Cramer's $V = 0.140$, $P = 0.003$), *Human Intrusions and Disturbance* ($\chi^2(3) = 71.5$, $P < 0.001$; Cramer's $V = 0.320$, $P < 0.001$), *Invasive and Other Problematic Species and Genes* ($\chi^2(3) = 49.1$, $P < 0.001$; Cramer's $V = 0.265$, $P < 0.001$), and *Pollution* ($\chi^2(3) = 17.6$, $P = 0.001$; Cramer's $V = 0.159$, $P = 0.001$).

PCoA revealed three main species groupings based upon threatening process categories (Fig. 2): one discrete cluster of species impacted only by *Biological Resource Use* (mostly species of *Nepenthes*), one discrete cluster of species impacted only by *Natural Systems Modifications* (mostly Australian species of *Drosera* and *Byblis*), and one large, poorly-defined cluster comprising species impacted by multiple threatening process categories. Analyses suggest that many ecosystems harbouring CPs face multiple concurrent (and likely interrelated) threats from *Residential and Commercial Development*, *Agriculture and Aquaculture*, *Energy Production and Mining*, *Transportation and Service Corridors*, *Human Intrusions and Disturbance*, *Invasive and Other Problematic Species and Genes*, *Pollution* and *Climate Change and Severe Weather*. The two discrete clusters suggest that *Biological Resource Use*, *Natural Systems Modifications* and *Geological Events* likely represent threatening processes to species occurring in predominantly ecologically intact ecosystems further from human development.

4. Discussion

The majority of CPs occupy highly-specific and often highly-specific ecological niches (Brewer and Schlauer, 2018), within sensitive habitats in areas experiencing conflict with anthropogenic land use and development. Most CP species are reliant upon the maintenance of natural ecosystem processes such as hydrology and fire for recruitment and population maintenance, and decline rapidly following disturbance to these processes. Many occupy restrictive niches, such as montane habitats, or persist in small, fragmented habitat remnants, and have no refugia in the face of global climatic change. Even where refugia are available, it is uncertain to what extent environmental change may impact the complex biological mutualisms and dietary specialisations upon which many CPs rely (e.g., Clarke et al., 2009; Greenwood et al., 2011; Rembold et al., 2012). Many perennial taxa can take several years to reach reproductive maturity, for example *Cephalotus* (Cross et al., 2019), *Darlingtonia* (Meindl and Mesler, 2011), *Dionaea* (Smith, 1931), *Heliamphora* (D'Amato, 2013), *Nepenthes* (A. Fleischmann, pers. obs.), *Roridula* (A. Fleischmann, pers. obs.), *Sarracenia* (Slack, 1980), *Triphyophyllum* (Cross et al., 2018a) and very likely all species of *Philcoxia* (A. Scatigna pers. comm.). As these genera harbour a high proportion of the CP species at risk of extinction, we contend that the high degree of ecological specialisation exhibited by many CP species likely places them at significant and imminent risk from anthropogenic change. We identify five significant outcomes from examination of the conservation assessments of CPs:

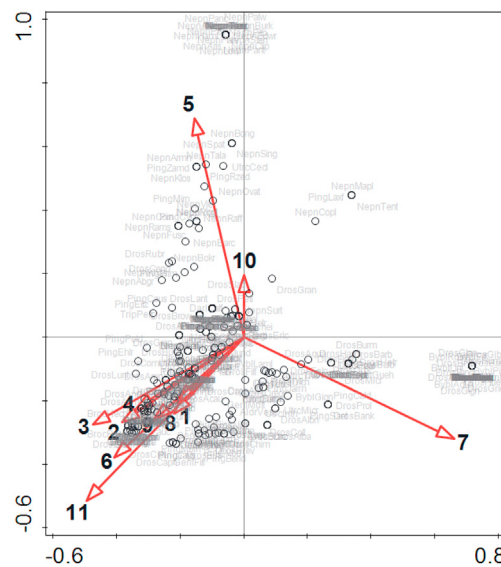


Fig. 2. Principal coordinate analysis (based on Jaccard's distance) showing the ordination (projection of axes 1 and 2) of the threatening processes impacting carnivorous plant species (for 790 species where threatening process data are available). Threatening process categories are projected into the ordination space (perpendicular projection of these categories to the axes provides an estimate of the correlation coefficient of that variable with that axis), and the distance of species and threat categories from the origin indicate relative importance in the biplot. 1- Residential and Commercial Development. 2- Agriculture and Aquaculture. 3- Energy Production and Mining. 4- Transportation and Service Corridors. 5- Biological Resource Use. 6- Human Intrusions and Disturbance. 7- Natural Systems Modifications. 8- Invasive and Other Problematic Species and Genes. 9- Pollution. 10- Geological Events. 11- Climate Change and Severe Weather.

- i) Species occurring in habitats in close proximity to, or which are regularly accessed by, people (i.e., *Aldrovanda vesiculosa*, *Cephalotus follicularis*, *Dionaea muscipula*, most lowland *Nepenthes*, *Philcoxia*, *Sarracenia*, and many species of *Drosera*, *Genlisea* and *Pinguicula*) are threatened by direct human activities such as the clearing of habitat for agricultural and residential development, as well as secondary impacts such as pollution and invasive species;
- ii) Many species occurring even in habitats distant from human development are threatened by alteration to natural ecosystem processes such as fire regimes and hydrological functioning;
- iii) Species occurring in remote regions or in habitats generally unsuitable for development (i.e., highland *Nepenthes*, *Heliamphora*) are often threatened by activities such as illegal logging and mining;
- iv) The most unique, spectacular, and horticulturally interesting species (i.e., *Cephalotus follicularis*, *Dionaea muscipula*, most *Sarracenia* and many species of *Nepenthes*) continue to be threatened by illegal collection for horticultural trade;
- v) Many species of CPs may be at risk of extinction in the face of global climatic change, particularly species adapted to, and thus reliant upon, highly specific habitats or inhabiting restricted ecological niches (i.e., species occurring in seasonally-wet and ephemeral aquatic habitats, and montane and high-elevation species of *Drosera*, *Nepenthes* and *Pinguicula*).

5. Habitat loss and land use change

5.1. Residential and Commercial Development

Residential and Commercial Development represents a rapid and permanent loss of habitat, often also leading to secondary threats such as weed invasion and alteration to natural ecological processes in surrounding ecosystems. While clearing for development threatens CPs in many regions (Fig. 3), its scale varies considerably. Urban development in cities in Sierra Leone, West Africa, has cleared significant *Triphyophyllum peltatum* habitat (A. Fleischmann pers. obs.; Fig. 3A) Development servicing tourism activities (e.g., mountain resorts in areas such as the Genting Highlands, Peninsular Malaysia) has been identified as a threat to *N. ultra* in the Philippines (Cheek and Jebb, 2013), and likely also affects numerous other *Nepenthes* from Southeast Asia (Clarke et al., 2018; Fig. 3B).

Rapid expansion of the Perth metropolitan area has resulted in substantial habitat loss (Ramalho et al., 2014; MacLachlan et al., 2017), despite the location of the city in one of the world's most biodiverse and endemism-rich floristic regions (Clarke et al., 2018). Significant development has occurred around the Swan and Canning Rivers, which once harboured large areas of low-lying, seasonally-wet heathland supporting diverse vegetation including many CPs (Lowrie, 2014; Cross, 2019). Lowrie (1981) noted that up to 18 species of *Drosera* and *Utricularia* co-occurred with *Byblis gigantea* in the swampland fringing the Canning River, and this area once harboured most of the habitat suitable for the CR *B. gigantea* (Cross et al., 2013). By 1981,

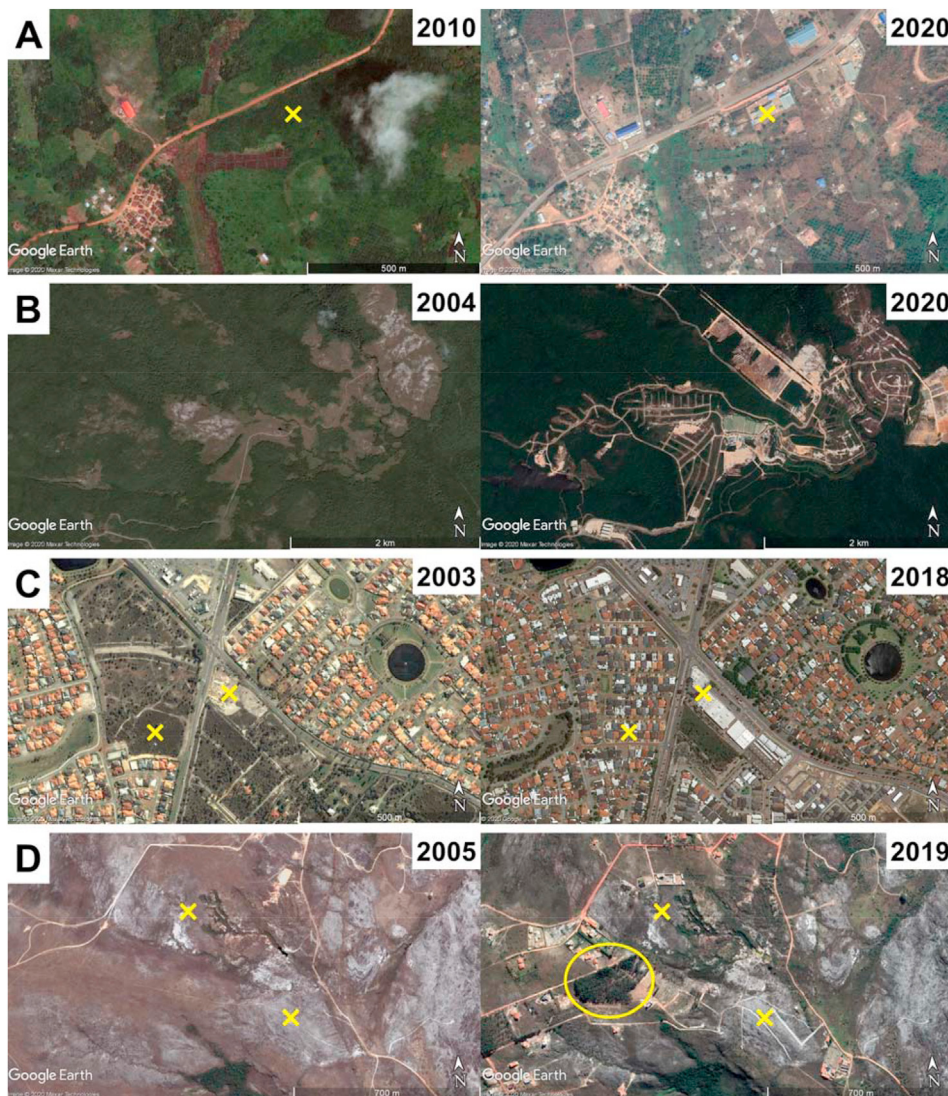


Fig. 3. Examples of small-scale destruction of carnivorous plant habitats resulting from urban development in the last two decades. **A** Africa: *Triphyophyllum peltatum* (DD, site of secondary rainforest in Sierra Leone personally observed by A. Fleischmann in 2006 indicated by a yellow “x”); **B** Asia: *Nepenthes bokorensis* (CR, previously occurred across the entire illustrated area, which is the type location in Cambodia, pers. obs. by A. Robinson in 2011); **C** Australia: *Byblis gigantea* (CR, extinct sites in Perth indicated by yellow “x”, last observed in 2003; Lowrie, 2014; Cross, 2019); **D** South America: *Drosera schwackei* (EN, threatened sites in Minas Gerais, Brazil indicated by yellow “x”, pers. obs. by P.M. Gonella and A. Fleischmann in 2018). The yellow circle in this image indicates the location of a *Eucalyptus* plantation. Satellite images © Google Earth 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

much of this swampland had been developed for housing and a shopping complex (Lowrie, 1981), but development continues in the region and has resulted in the extinction of *B. gigantea* from the Swan Coastal Plain (Fig. 3C; Cross, 2019). *Byblis gigantea* now persists in only four populations in the Darling Range east of Perth, which continue to decline in the face of altered hydrological and fire regimes (Lowrie, 2014; Cross et al., 2018b; Cross, 2020e). Urban expansion and associated habitat degradation on the Swan Coastal Plain has also caused declines in the extent of *Drosera gigantea* and *Utricularia menziesii* (Cross, 2019), as well as for many other specialised flora including orchids (Newman et al., 2015). Continued urban expansion of the town of Albany on the south coast of Western Australia is encroaching on sensitive peat swamp habitats, threatening the VU *Cephalotus follicularis* (Cross et al., 2018b, 2019).

Rather paradoxically, the development of a settlement known as “Sundew Villas” is encroaching on and replacing botanically diverse *fynbos* habitat harbouring numerous *Drosera* species near the town of Hermanus, coastal Western Cape of South Africa (S. McPherson pers. comm.; A. Fleischmann pers. obs. 2006). Similarly, development around the town of Darling has resulted in local extinctions of *Drosera cistiflora* and the VU *D. pauciflora* as well as several endemic geophytes (E. Green pers. comm.; A. Fleischmann pers. obs.) in an area of Western Cape *renosterveld* vegetation celebrated for a particularly high

rate of endemism. The expansion of the city of Diamantina in southeastern Brazil, situated in the diverse and high-endemism *campos rupestres*, has impacted at least 15 CP species including the EN local-endemic *Drosera schwackei* (Fig. 3D) and VU *Drosera spiralis* (P.M. Gonella and A. Fleischmann, pers. obs.). Remnant CP habitat in the region continues to be degraded by alteration to natural fire and hydrological regimes, which have facilitated weed invasion (Barbosa et al., 2010), particularly the recurrent use of fire for vegetation clearance and the maintenance of pasture for cattle grazing around urban settlements.

Habitat destruction for development is recognised as the most significant threat faced by *Dionaea* and all species of *Sarracenia* in the USA (Schnell, 2002; Luken, 2012; Clarke et al., 2018). Large areas of undisturbed CP habitats remain on privately-owned land in the region, and although most CP species being protected under federal or national laws in the United States, these protections offer minimal protection on private land where it is both legal and often profitable to destroy habitat harbouring protected species such as *Sarracenia* (Meyers-Rice, 2001). Large populations of *Sarracenia* continue to be cleared by landowners for commercial and domestic development, for example in pine forest habitats in northern Florida (Schnell, 2002; Rice, 2006; Clarke et al., 2018).

5.2. Agriculture and aquaculture

Logging, particularly illegal logging, represents a significant ongoing threat to CPs in tropical regions (Fig. 4A). Logging of primary and secondary rainforest represents a significant threat to the remaining populations of *Triphyophyllum peltatum* (as well as the closely-related but non-carnivorous *Habropetalum*) in tropical West Africa (Munro, 2009; Cross et al., 2018b). Illegal logging has been identified as a threat to *Nepenthes* species from Cambodia (Mey et al., 2010), Indonesian Borneo (Giesen, 2000; Meijaard et al., 2005), and throughout the Philippines (Amoroso et al. 2009, 2017; Gronemeyer et al., 2014; Cheek et al., 2015; Lagunday et al., 2017, Lagunday and Amoroso, 2019). The discovery of undescribed *Nepenthes* species and new populations of known species along the margins of logging roads and in areas made accessible by logging activities—for

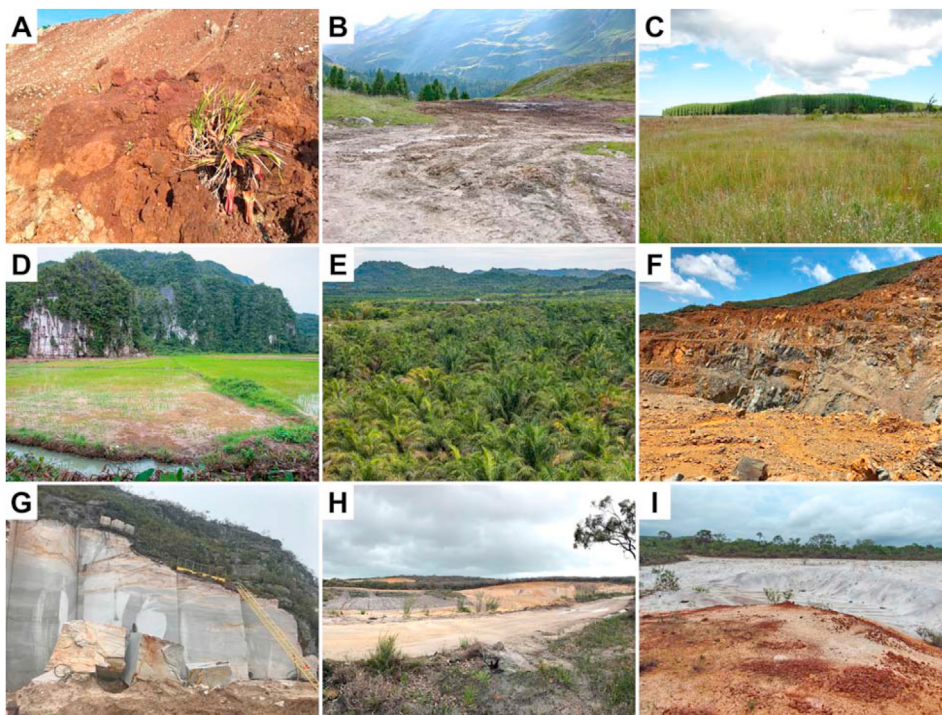


Fig. 4. Examples of the degradation and destruction of carnivorous plant habitats from agricultural and development practices (A–E) and mining activities (F–I). **A.** Clearance of coastal forest for deluxe housing near Jayapura, Papua Province, Indonesian New Guinea, has destroyed a well-known, local stronghold of *Nepenthes neoguineensis* (Photo: A. Robinson, 2016). **B.** Alpine seepage habitat of *Pinguicula leptoceras* paved for a winter sports area in the state of Tyrol, Austria (Photo: A. Fleischmann, 2008). **C.** *Eucalyptus* plantations in areas of *campos rupestres* in the Serra do Cabral, a biodiversity hotspot for CPs in Minas Gerais, Brazil (Photo: F. Nepomuceno da Costa, 2012). **D.** Subsistence padi monoculture abuts a karst formation of special scientific interest in northern Palawan (Philippines), home to three endemic CPs and numerous other endemic plants protected only by the extreme topography (Photo: A. Robinson, 2011). **E.** Young oil palm plantation at a habitat of *Nepenthes sumatrana* near the North Sumatra (Indonesia) coast where seven individuals of this CR species persist (Photo: A. Robinson, 2017). **F.** A nickel extraction pit in northern Mindanao (Philippines), the scrub to the rear is the only known habitat of a CR endemic *Nepenthes* (Photo: A. Robinson, 2018). **G.** Quartzite mining of seepage areas in the municipality of Diamantina (Brazil) threatens several micro-endemic species of the *campos rupestres* including the EN *Drosera schwackei* (Photo: K. Henrique da Silva, 2018). **H.** A sand quarry on the Bass Coast (Victoria, Australia) threatening the southernmost remnant of native vegetation in the >95% cleared West Gippsland region harbouring numerous *Drosera* and several threatened orchid species (Photo: A. Robinson, 2019).

example, *N. dactylifera*, *N. ehippiata*, *N. fractiflexa*, *N. glandulifera*, *N. pitopangii*, *N. platycheila* and *N. vogelii*, among others (Lee 2004; Lee et al., 2009; Robinson et al., 2019a; Golos et al., 2020; A.T. Cross and A. Robinson pers. obs.)—has led to an indisputable observation bias of *Nepenthes* in anthropogenic ruderal habitats, and occasional but not necessarily correct assertions that these plants might actually benefit from such disturbance (discussed in Golos et al., 2020). However, these species are naturally often overwhelmingly epiphytic, and while many *Nepenthes* certainly proliferate in disturbed sites (typically in the company of resam fern *Dicranopteris linearis*, Gleicheniaceae), repeated visits to ruderal habitats that do not undergo periodic maintenance (slashing, mowing etc.) show that *Nepenthes* are often ephemeral and the succession of secondary growth eventually renders conditions unfavourable for their survival (A. Robinson pers. obs.). Since it is extremely difficult to survey epiphytic species assemblages in undisturbed forest across a wide area, it is not readily possible to compare the relative numbers of *Nepenthes* growing unseen in pristine forest canopy with those occasionally proliferating along roadsides in logged areas. However, continued logging can only further erode biodiversity and remove trees large and sheltered enough to harbour sequential generations of larger, relatively desiccation-intolerant epiphytes such as *Nepenthes*. Small-scale clearing in mountainous areas in Europe also threatens CPs such as montane *Pinguicula* (Fig. 4B).

Plantations of rapid-growing *Eucalyptus* and *Pinus* established for timber and pulp production represent a major threat to CPs in the *campos rupestres* grasslands of Brazil (Rapini et al., 2008). In addition to habitat clearing for afforestation, *Eucalyptus* have relatively high evapotranspiration rates and can markedly alter local soil hydrology in ecosystems around the world (e.g., Zhou et al., 2002; Engel et al., 2005; Benyon et al., 2006; Shi et al., 2011; Ribas et al., 2016). Leaf litter from both *Eucalyptus* and *Pinus* is toxic to native flora and soil biota through allelopathic effects (Rizvi et al., 1999; da Silva Rodrigues-Corrêa et al., 2017), and their growth form can result in heavy shading which affects the open grassland habitat inhabited by the NT *Drosera viridis* (Gonella and Lehn, 2020). Additionally, cultivated *Pinus* species (usually *Pinus elliotii* and *P. taeda*; Zenni and Ziller, 2011) can become invasive in local ecosystems, and the linear infrastructure for large forest monocultures further fragments habitat, reducing genetic connectivity between populations of native species (Ribas et al., 2016). Several CR and EN CP species are threatened by *Eucalyptus* afforestation in Brazil (Fig. 4C), including *Genlisea metallica* and *G. oligophylla* (Fleischmann et al., 2011), *Philcoxia rhizomatosa* (Scatigna et al., 2015), and *Drosera magnifica* (Gonella et al., 2015).

At larger scales, the cultivation of rice (typically *Oryza sativa*) and, more recently, oil palm (*Elaeis guineensis*), has destroyed large areas of tropical and subtropical lowland habitat in Southeast Asia (Fig. 4D and E). Rice cultivation has primarily affected CPs in Indochina, the rice bowl of Asia and one of the most ancient agrarian landscapes on Earth; *Drosera*, *Utricularia* and *Nepenthes* in Cambodia, Vietnam and Thailand now persist predominantly in marginal habitats, ruderal habitats, rocky or sandy mineral soils in seasonally wet veals (savannahs) ill-suited to farming, and occasionally in reserves (A. Robinson pers. obs.). The farming of hill rice in the dramatic mountainside terraces of great cultural importance in the cordillera of Benguet and Ifugao (Luzon, Philippines) has destroyed significant areas of montane forest (A. Robinson pers. obs.). The clearing of natural forest for monocultures of structurally homogeneous oil palm are associated with major declines in biodiversity and species richness throughout southeast Asia (Fitzherbert et al., 2008; Fig. 4E), and although the rate of conversion of natural forest to plantation has slowed in recent years, this monoculture remains the dominant agricultural land cover type in Sumatra and Borneo (Gaveau et al., 2016; Austin et al., 2017). Both islands are recognised centres of *Nepenthes* biodiversity (see e.g., Clarke, 1997), and a variety of lowland *Nepenthes* are associated with peat forests and associated *kerangas* (heath forest). The proportion of peat forest cover in Sumatra fell from 75% to 28% between 1990 and 2010, almost entirely to make way for oil palm plantations (Miettinen et al., 2018). Over 60% of populations of the VU Bornean *N. bicalcarata* populations have been lost to the conversion of peat-swamp forests to palm oil monocultures in the last three decades (Clarke et al., 2018), and the majority of suitable habitat for the CR Sumatran endemic *N. sumatrana* has been cleared for oil palm and human settlement (A. Robinson, pers. obs.; Fig. 4E). While widespread species such as *N. ampullaria*, *N. gracilis* and *N. rafflesiana* are still considered LC, the abundance of these species has plummeted due to habitat clearance. In Sierra Leone, clearing for oil palm plantation has destroyed most known localities of the rare and poorly-protected *Triphyophyllum peltatum* (A. Fleischmann pers. obs.; Fig. 3A), and deforestation has resulted in this species facing a high risk of extinction throughout large parts of its natural distribution (Cross et al., 2018b).

In few regions are the broad-scale effects of land use change so well-documented as in Australia. Australia is especially notable for its carnivorous flora, being home to nearly a third of all CPs (245 species from six genera), of which more than half (124 species) are endemic to the Southwest Australian Floristic Region (SWAFLR; Robinson et al., 2017; Clarke et al., 2018). The majority of these species evolved within the *kwongan* shrublands, an extensive, geologically and climatically stable zone of severely phosphorous-impoverished soils. *Kwongan* comprises that region's most species-rich vegetation, harbouring approximately 70% of the ca. 8000 native plant species recorded from the SWAFLR, and thus a significant proportion of the ca. 13,000 total native species recorded from all of Western Australia (Hopper and Gioia, 2004; Robinson, 2019). Western Australia's Wheatbelt, which sits within the SWAFLR, has among the highest rates of habitat clearance on the planet; for example, around 97% of all native vegetation has been cleared in the Avon wheatbelt region (Saunders, 1989; Bradshaw, 2012). This clearing continues, and habitat loss, fragmentation and degradation represent real and ongoing threats to native flora in the region.

Fewer than 5–20% of remaining native vegetation is retained in protected areas for almost all SWAFLR bioregions (Clarke et al., 2018). As many narrowly endemic CP species from the SWAFLR have only been discovered and described in the past 20–30 years (Lowrie, 2014), the high extent of habitat loss suggests that some species may have been driven to extinction before they could have been discovered (Clarke et al., 2018). Among the CPs endemic to the SWAFLR are four assessed as CR (*Byblis gigantea*, *Drosera allantostigma*, *D. leioblastus*, *D. oreopodion*), one NT (*Utricularia westonii*) and 15 VU species. The three

Drosera species are arguably the most threatened of these, with *D. oreopodium* known from just one extant population comprising several hundred individuals occupying ca. 25 m² (Clarke et al., 2018; A. Cross, T. Krueger, A. Robinson pers. obs. 2017–2020), *D. leioblastus* known from a single declining population of seven individuals in 2020 down from 20 individuals in 2019 (T. Krueger pers. obs.), and *D. allantostigma* potentially EW as surveys in both 2019 and 2020 failed to locate any individuals at the single known locality following severe drought and habitat degradation (Cross, 2020a; T. Krueger pers. obs.). Similar declines in suitable habitat can be observed on both the local scale of apparent micro-endemics (e.g., *D. leioblastus*), but also at regional scales as exemplified by *D. albonotata*; a species described and assessed as VU in 2018 based on its six small, extant populations (two previous collection sites now comprise farm and residential land, respectively) sparsely scattered across a relatively broad ca. 87 km corridor of extremely fragmented patches of remnant habitat within which it is likely to have once been widespread, if not reasonably common (Robinson et al., 2018). The significant issue of habitat clearance and fragmentation is further compounded by the marked advancement of diminishing rainfall levels from the arid Australian interior outwards through the Wheatbelt towards the coast (see *Global climatic changes*; also e.g., Gibson et al., 2008).

5.3. Energy Production and Mining

The impacts of *Energy Production and Mining* predominantly affect species of *Nepenthes* and *Pinguicula*, as species from these genera most commonly inhabit higher-elevation habitats on mineral-rich terranes that are the focus of mining activities, but are also felt in other significant mining provinces such as Brazil (Fig. 4G) and Australia (Fig. 4H). A number of *Nepenthes* species (e.g., *N. attenboroughii*, *N. erucoides*, *N. northiana*, *N. sumatrana*, *N. truncata*) are threatened by metal extraction from mafic areas, such as in northeastern Mindanao and Palawan (Philippines), eastern Sulawesi and the highlands of West Papua (Indonesia), or by quarrying for the concrete industry from limestone areas in western Sarawak and central Peninsular Malaysia (A. Robinson pers. obs.). Open-cast mining is listed as a specific threat to several *Nepenthes* in the Philippines including *N. ramos* and *N. ultra* (Cheek and Jebb, 2011, 2013), while nickel mining is a threat to *N. erucoides* and *N. truncata* in the Philippines (Robinson et al. 2019b), *N. halmahera* and *N. weda* in Indonesia (Cheek, 2015), and limestone quarrying and coal mining are regarded as serious threats to *N. khasiana* in India (Prasad and Jeeva, 2009; Singh et al., 2011). Environmental impact assessments are poor or non-existent in many of these regions, and rarely consider biodiversity (Bravante and Holden, 2009); indeed, Bravante and Holden (2009) note that, in a 2005 interview, Attorney Grizelda Mayo-Anda, the Executive Director of the Environmental Legal Assistance Centre (ELAC) in Palawan, “related how there was an endangered carnivorous pitcher plant in an area that was scheduled to be a mining project; when she pointed this out to the engineers in charge they merely laughed at the suggestion that the project should not proceed because of a plant.” Such attitudes appear to be deeply ingrained in countries such as Indonesia and the Philippines, where ineffective law enforcement has resulted in the inadequate protection of threatened species even when they occur completely within the boundaries of protected areas (Gaveau et al., 2009; Clarke et al., 2018).

A number of *Pinguicula* species are impacted by mining activities in Central and South America, commonly from the quarrying of gypsum and other limestone terranes. For example, in Mexico *P. gracilis* occurs in a region aggressively quarried for limestone in order to provide for the needs of the burgeoning industrial centre of Monterrey (Nuevo León) and to supply the nearby United States (Lampard et al., 2016), while mining has destroyed and fragmented the habitat of *P. albida*, *P. cubensis* and *P. filifolia* in western Cuba (Domínguez et al., 2014). The construction of hydroelectric dams pose serious threats to habitats of some microendemic *Pinguicula* species in Mexico by flooding their habitats or altering their hydrology (e.g., *P. elizabethiae*, *P. moctezumae*—ironically, the latter species was initially discovered during species inventories before the building of the large Zimapán Hydroelectric Dam; Lampard et al., 2016; Fleischmann and Rocca, 2018). All species of *Philcoxia* are severely or potentially impacted by mining, being restricted to one to only a few populations on deep sand banks from which sand is extracted for construction purposes (Taylor et al., 2000; Scatigna et al., 2015, 2016a, 2016b, 2017; Fig. 4I). Habitats of *Philcoxia* have also been historically used for diamond prospecting (Taylor et al., 2000), and the CR *Philcoxia coureensis* occurs in an area with potential for construction of hydroelectric plants (Scatigna et al., 2017).

Although poorly documented, both legal and illegal mining activities also impact CP habitats in regions such as South America, tropical Africa and Madagascar, and may increasingly represent threats to species of *Drosera*, *Genlisea*, *Heliophora*, and *Utricularia* into the future. For example, illegal mining on Venezuelan tepuis (e.g., Sharpe and Rodríguez, 1997) may threaten species of *Heliophora* and *Brocchinia* (McPherson, 2008). Mining, and often illegal mining activities, threatens many protected areas throughout Africa (e.g., Laurance et al., 2006; Tranquilli et al., 2014; Boadi et al., 2016), and is a significant driver of habitat loss in Madagascar (e.g., Cardiff and Andriamanalina, 2007; Watson et al., 2010). These activities are often undertaken in regions known to harbour remnant CP habitat, and authors have previously noted inadequacies in the implementation and enforcement of environmental protection legislation in these jurisdictions (e.g., Sarrasin, 2006; Andrews, 2015).

5.4. Transportation

In some regions, such as areas of the SWAFLR where residential development and agricultural clearing has resulted in the loss of more than 97% of natural vegetation (Clarke et al., 2018), road and railway reserves comprising narrow, linear bands of remnant vegetation (corridors) are of significant conservation value (Saunders and Hobbs, 1991), and represent the only

remaining habitat for several CP species. For example, the CR (or possibly EW) *Drosera allantostigma* is known only from road verge habitat near Badgingarra, ca. 200 km north of Perth (Cross, 2020a), while the CR *D. oreopodion* is known only from a narrow strip of unprotected remnant vegetation directly adjacent to a railway line near Armadale, southeast of Perth (Cross, 2020b). The high susceptibility of narrow transportation corridors to disturbance places both species at high risk of rapid population declines and possibly extinction. *Drosera allantostigma* is threatened by drought, altered hydrology, eutrophication, weed invasion and road maintenance activities (Lowrie, 2014; Cross, 2020a; T. Krueger pers. obs.), and may already be extinct in the wild; the species is self-incompatible (A. Fleischmann, M. Meisterl, unpubl.), and such a small population size likely compromised capacity for soil seed bank formation (considered an important drought-avoidance strategy for species in the *D. nitidula* complex, to which *D. allantostigma* belongs; Lowrie, 2014). *Drosera oreopodion* is threatened primarily by weed invasion, although paradoxically is also likely threatened by the spraying of glyphosate for weed management at the site (Cross, 2020b).

The construction of transportation corridors through or adjacent to ecologically-sensitive habitats such as wetlands can markedly alter natural ecological processes such as hydrology, causing rapid declines in ecologically-specialised species such as CPs. For example, road development through coastal swampland near Esperance, Western Australia, resulted in the extirpation of a population of *Aldrovanda vesiculosa* (at the time, the only population known from southwestern Australia; Cross, 2012a). Similarly, the type location of the CR Brazilian endemic *Philcoxia goiasensis* was destroyed for road construction in late 1970s (Scatigna et al., 2016a), and road construction has also been implicated as a major cause of population declines for the VU *Dionaea muscipula* and most species of *Sarracenia* in the United States (Schnell, 2002). Road maintenance has caused population declines or local extinction in *Pinguicula*, for example the single Italian locality of *P. hirtiflora* in Calabria (Peruzzi et al., 2004) and a site of the CR *P. reichenbachiana* in the Roya Valley along the French-Italian border (A. Rocca, pers. comm.; A. Fleischmann, pers. obs.).

Occasionally, the maintenance of linear infrastructure and associated reserves such as tracks, roads, and power-line rights of way (where herbicide is not used as a management tool) can create habitat for ruderal CP species. Documented examples include *Sarracenia* and *Drosera* in the United States (Sheridan et al., 1997), *Nepenthes* such as *N. gracilis* and *N. rafflesiana* in southeast Asia (Clarke, 1997; Clarke et al., 2018), and numerous species of *Drosera* in Western Australia (particularly *D. glanduligera* and some pygmy *Drosera*; Lowrie, 2014), South Africa (A. Fleischmann pers. obs.) and Brazil (e.g. *D. latifolia* and *D. montana*; Gonella et al., 2014; Rivadavia et al., 2014). Several Mexican *Pinguicula* are also known to occur on roadside habitats (e.g., Lampard et al., 2016). Road maintenance activities can impact populations of lithophytic and ruderal species exploiting new habitat created by road construction (e.g., the Alpine-endemic *P. poldinii*, which was initially discovered on a newly-created seepage following road development; Casper and Steiger, 2001).

6. Habitat degradation and alteration to natural ecological processes

6.1. Eutrophication

The eutrophication of wetlands represents a major threat to palustrine and aquatic biodiversity around the world. Long histories of agricultural land use in areas such as Europe have not only cleared significant habitat for aquatic CPs such as *Aldrovanda vesiculosa* and numerous *Utricularia* (e.g., Cross, 2012a; Adamec, 2018, 2020), but have also left a legacy of eutrophic wetland habitats (Lamers et al., 1998; Smith, 2003). The vast majority of CPs occur in oligotrophic habitats, particularly under nitrogen(N)-limited conditions (Brewer and Schlauer, 2018). Elevated [N] in soil or water is deleterious to CPs as it increases competition from other plants or algae and may induce abiotic stress through ammonium toxicity (Brewer et al., 2011; Cross, 2012a; Abbott and Brewer, 2016). The eutrophication of wetland habitats is recognised as a major threatening process for aquatic CPs such as *Aldrovanda vesiculosa* (Cross, 2012a) and numerous species of *Utricularia* (e.g., Vaithyanathan and Richardson, 1999; Adamec, 2020). N-inputs from agricultural fertiliser runoff and aerial N-deposition can eutrophy semi-aquatic and even terrestrial habitats (Fig. 5), and have been shown to deleteriously affect CP species including *Darlingtonia californica* (Grandy, 2018), *Drosera rotundifolia* (Millett et al., 2012, 2015), and *Sarracenia purpurea* (Gotelli and Ellison, 2002). Significant CP population declines have been reported following N fertilisation in natural habitats (Redbo-Torstensson, 1994), as N-deposition also drives shifts in species composition and productivity and can facilitate weed invasion (Berendse et al., 2001).

6.2. Altered fire regimes

Fire is a natural process in many habitats harbouring high CP diversity, such as the Brazilian *cerrado* and *campos rupestres*, the Cape *fynbos* and related vegetation types, Australian *kwongan*, and most mediterranean regions (Bradshaw et al., 2018). Fire is also recognised as an integral process in the reproductive biology and population maintenance of many CP species (e.g., Cross et al., 2013, 2017, Cross et al., 2018b, 2018c). However, fire management must allow for the idiosyncratic and highly variable responses to different fire regimes exhibited by different species and communities (Burrows, 2008). Global climatic changes are driving an increase in the frequency, severity, and spatial extent of wildfires in biomes around the world, and fire-management strategies typically comprise total fire suppression or aseasonal prescribed burning at higher frequency than the occurrence of natural fires (often at <3–7-year return intervals; Bradshaw et al., 2018). There is considerable evidence that

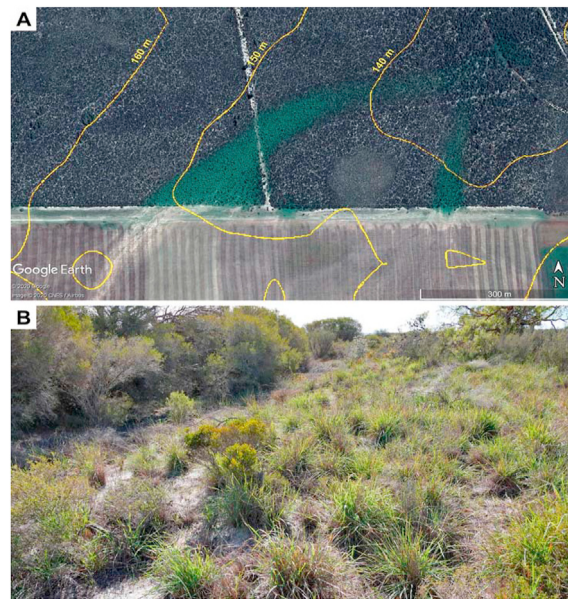


Fig. 5. **A.** Eutrophication caused by runoff from nearby farmland (lower third of the image) supports subsequent grassy weed invasion of seasonally wet depressions (above) in heathland habitats inhabited by numerous CP species near Badgingarra, Western Australia. These processes can be observed from satellite imagery at numerous locations in the area as bright green runoff smears. Contour lines and annotated numbers indicate elevation (m above sea level). Satellite imagery © Google Earth 2020. **B.** Seasonally-wet sand plain overgrown by invasive grasses following eutrophication at the type and only known location of *D. allantostigma* (Photo: T. Krueger 2020). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

high-intensity fires (often compounded by higher fuel loads from invasive grasses), aseasonal burning, short fire intervals, and fire suppression can deleteriously impact numerous CP species and the ecosystems upon which they rely (Fig. 6A).

High-intensity fires represent a greater stochastic impact to perennial non-geophytic species lacking underground storage organs (e.g., pygmy *Drosera*, *D. sect. Bryastrum*). Geophytes such as tuberous *Drosera* (*D. sect. Ergaleium*) can persist through even high-intensity fires before resprouting from underground tubers (with pyrogenic flowering even reported for some species; Cross et al., 2018b), unless fires are aseasonal and occur during periods of active growth in winter and spring. In contrast, species lacking underground storage organs such as pygmy *Drosera* are generally fire-killed, and populations are likely more susceptible to significant fluctuations under altered fire regimes (Lowrie, 2014; A. Fleischmann and T. Krueger pers obs. 2008–2020), particularly when the impacts of increased fire frequency or intensity compound existing environmental stresses such as drought (Bradshaw et al., 2018; Cross et al., 2019). For example, an intense bushfire in 2006 killed almost all individuals in the only known population of the CR *Drosera leioblastus*, with only 11 individuals rediscovered at the site in 2008, and total population size fluctuating between 6 and 20 individuals since then (Cross, 2020c; A. Fleischmann and T. Krueger pers obs. 2008–2020). A similarly intense bushfire burned through more than a third of Stirling Range National Park in December 2019, affecting eight of the ten recorded (sub-)populations of the VU *D. gibsonii*; all individuals were killed in two (sub-)populations, while moderate to severe population declines occurred in most others (T. Krueger pers obs. 2020; Fig. 6B). Only two (sub-)populations comprising several hundred individuals were unaffected by the fire. Although *D. gibsonii* is known to recover slowly from seeds following fire (Cross, 2020d), the large observed population size declines likely increase susceptibility to droughts or recurrent fires at short intervals (e.g., prescribed burns; Cross, 2020d). Significant fluctuations in the population size of the Brazilian CR *Drosera graminifolia* were also observed following an unusually intense wildfire in the late 1990s (Gonella et al., 2012).

Both short fire intervals and long-term fire suppression threaten the VU *Cephalotus follicularis* in southwest Western Australia; frequent fires likely jeopardise seed-based recruitment (Just et al. 2019), while fire suppression appears to have resulted in the loss of a population from the Haag Nature Reserve (Cross et al., 2019). Additionally, while *C. follicularis* is known to recover vigorously following summer wildfires (Lowrie, 2014), population declines have resulted from aseasonal fires and unusually intense fires causing damage to the peat soils supporting its *Callistemon glaucus*/*Homalospermum firmum* thicket habitat (Clarke et al., 2018; Cross et al., 2019; 6A). Fire suppression has also been implicated in population declines of the fire ephemerals *Byblis gigantea* (CR) from southwest Western Australia (coupled with hydrological change; Cross et al., 2013, Cross et al., 2018b; Cross, 2019) and *Drosophyllum lusitanicum* from the Mediterranean (Correia and Freitas, 2002; Paniw et al., 2017), as well as for CPs from fire-prone pine savannah in the United States including *Dionaea muscipula* (Luken, 2012) and numerous species of *Sarracenia* (Godt and Hamrick, 1996; Murphy and Boyd, 1999; Wang et al., 2004). Short fire intervals, aseasonal fires and fire suppression in *fynbos* habitats are likely deleterious to *Roridula gorgonias* and *R. dentata* (Hall, 1987). Inappropriate fire management is also recognised as a key threat to several species of *Philcoxia* from Brazil (Scatigna et al.,

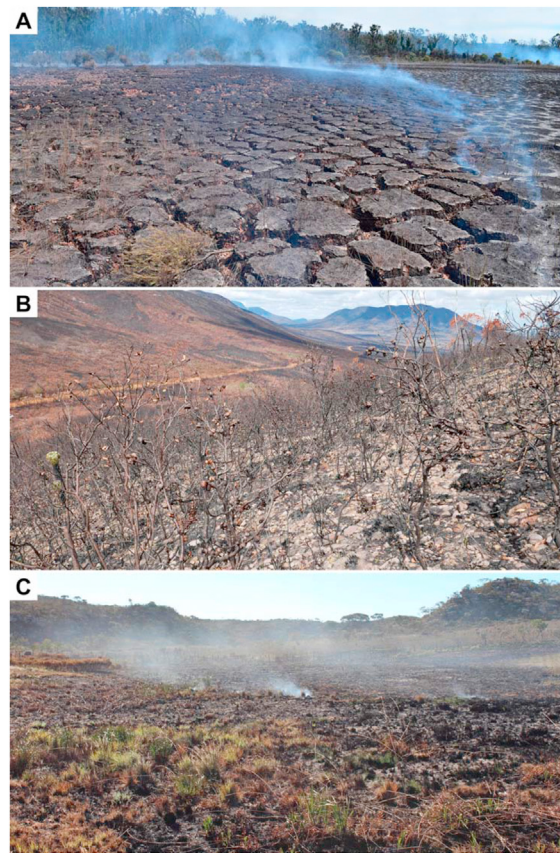


Fig. 6. CP habitats affected by high-intensity fires. **A.** Peat swamp habitat of the VU *Cephalotus follicularis* burned by a high-intensity bushfire in January 2018 near Albany, Australia. The *Cephalotus* population appears to have been extirpated by the fire, which was started by a prescribed burn and resulted in the loss of peat beds accumulated over a period of ~5000 years (Bradshaw et al., 2018; Photo: D. Edmonds, 2018). **B.** Burned heathland habitat of the VU *Drosera gibsonii* following a high-intensity bushfire in Stirling Range National Park, Australia, during December 2019. No *D. gibsonii* individuals could be located at fire-affected populations in March 2020 and it remains unclear whether a viable soil seed bank remains from which population recovery could occur (Photo: T. Krueger, 2020). **C.** Burnt habitat of numerous *Drosera*, including the EN *D. ascendens*, VU *D. camporupensis* and VU *D. spiralis*, in Parque Nacional das Sempre Vivas, Brazil, after a fire which was illegally started by farmers (Photo: F. Nepomuceno da Costa).

2016a, 2016b; Cross et al., 2018b), and short fire intervals are considered a threat to the newly-described *Drosera buubugujin* from tropical northeastern Australia (Mathieson and Thompson, 2020).

6.3. Altered hydrological regimes

It is well known that the majority of CPs are restricted to habitats that are ‘sunny, moist, and nutrient poor’ (e.g., Brewer and Schlauer, 2018; Skates et al., 2019). Indeed, most species are restricted to seasonally- or permanently-wet freshwater habitats, and many are finely tuned to particular hydrological regimes and exhibit specific ecological requirements centred upon moisture availability (e.g., Robinson et al., 2017; Brewer and Schlauer, 2018; Cross et al., 2019). Waterlogged and moisture-retaining soils in regions such as the SWAFLR provide habitat for numerous phylogenetically relictual taxa such as CPs (Hopper and Gioia, 2004), and carnivory likely confers a competitive advantage in wetland habitats (e.g., Brewer et al., 2011). However, natural hydrological regimes can be extremely sensitive to disturbances from land use change (e.g., from the clearing of native vegetation or afforestation), not only at local scales but also throughout catchment areas (Fohrer et al., 2001), placing species reliant upon narrow hydrological niches at high intrinsic risk from any processes impacting natural ecological processes.

In southwest Australia, hydrological change resulting from agricultural and urban development (i.e. abstraction and reduced water flow into wetlands) has been implicated directly in population declines for *Utricularia helix* (Lowrie et al., 2014), the VU *Cephalotus follicularis* (Cross et al., 2018b, 2019; Just et al., 2019), and the CR *Byblis gigantea* (Cross et al., 2013; Cross et al., 2018b; Cross, 2019). Alteration to natural hydrological regimes resulted in the localised extirpation of the EN *Aldrovanda vesiculosa* in southern Western Australia following road development (Cross, 2012a), and is also recognised as a threat to both *Darlingtonia californica* in the northwestern United States (Grandy, 2018) and species of *Sarracenia* in the southeastern United States (Furches et al., 2013). Hydrological change resulting from afforestation (*Eucalyptus* plantations)

threatens the EN *Drosera schwackei*, VU *D. spiralis*, CR *Philcoxia minensis* and *P. rhizomatosa*, as well as several other CP species from the *campos rupestres* in Brazil (Ribas et al., 2016; Scatigna et al., 2016b, 2017; P.M. Gonella, pers. obs.). Given that freshwater wetlands are among the most threatened and degraded ecosystems on earth (e.g., Reis et al., 2017), and that climatic and land use changes increasingly threaten the hydrological integrity of wetland habitats around the world (Junk et al., 2013), it seems probable that alteration to natural hydrological regimes will impact almost all CPs from mesic habitats to a greater or lesser extent in coming years.

In the European Alps, some wetland habitats inhabited by CPs are threatened by water collection and storage to supply the high-water demand of creating artificial snow to support winter tourism in a warming climate. In addition to the direct impact of reservoir development close to natural lakes or wetland sites, water collection can drain subjacent natural seepage habitats and bogs (De Jong, 2012), causing changes to soil and vegetation characteristics (e.g., OECD, 2007; Rixen and Freppaz, 2015; Pintaldi et al., 2017). For example, reservoir development for artificial snow production in Obergurgl, Austria, destroyed a large population of the Alpine-endemic *Pinguicula leptoceras* (Lampard et al., 2016). Several species of Mediterranean *Pinguicula* are threatened by the channeling of streams and seepage areas, as well as the tapping of springs for agriculture or water supply, such as *P. mariae*, *P. megaspilaea* (as *P. habilitii*), *P. poldinii*, and *P. reichenbachiana* (Yildirim et al., 2012; Lampard et al., 2016; A. Fleischmann, pers. obs.). These impacts are most strongly felt by species restricted to only permanently-wet seepage habitats in dry Mediterranean climates (Fleischmann and Rocchia, 2018), and will likely increase with rising demand for water in a drying climate.

6.4. Invasive species

Most CPs compete poorly with other vegetation, particularly woody perennials and annual grasses, and occupy ecological niches where competition is minimised (Gibson, 1983; Juniper et al., 1989; Brewer and Schlauer, 2018). Exotic species such as annual grasses can spread rapidly even within protected areas, outcompeting and displacing native flora and altering natural fire regimes (Alves and da Silva, 2011). Invasive species therefore represent a significant threat to CPs, and there are many examples globally of the deleterious impact of exotic weeds on CP populations. In Perth, southwestern Australia, competition from weeds including *Watsonia* spp. (Iridaceae), *Briza maxima*, *Ehrharta calycina* and *Eragrostis curvula* (all Poaceae) threatens the only known population of *Drosera oreopodion* (Cross, 2020b) as well as other species including *Drosera allantostigma* and *D. bulbigena* (T. Krueger pers. obs. 2014–2020; Fig. 5). Brazilian *cerrado* and *campos rupestres* habitats are threatened by invasive African grasses including *Melinis minutiflora* (Poaceae) (Pivello et al., 1999; Zenni and Ziller, 2011), which has been used as pasture for cattle farming (Dean, 2004) and was, until recently, even included in post-mining restoration programs (Ribeiro et al., 2017). CP species from the *campos rupestres* threatened by invasive grasses include the CR *Drosera graminifolia*, *D. magnifica*, *D. quartzicola* and *Philcoxia courensis* (Gonella et al., 2012; Gonella et al., 2015; Scatigna et al., 2017; P.M. Gonella, pers. obs.), the EN *D. ascendens*, *D. graomogolensis*, and *D. spirocalyx* (P.M. Gonella, pers. obs.), and numerous *Genlisea* species (Fleischmann et al., 2011). The introduction and naturalisation of Australian *Acacia*, including *A. saligna*, *A. pycnantha*, *A. longifolia* and *A. cyclops*, has significantly affected many seasonally wet, sandy, oligotrophic habitats in South Africa (e.g., *fynbos*, *sandveld* and *renosterveld*; van Wilgen et al., 2012). Dense thickets of N₂-fixing *Acacia* develop rapidly in these habitats, resulting not only in the overgrowth of indigenous vegetation but also increased soil [N] from the decomposition of N-rich leaf litter (Witkowski, 1991). *Acacia* develop extensive, long-lived soil seed banks making their control and removal challenging (van Wilgen et al., 2012; Strydom et al., 2019). Populations of *D. cistiflora* (including a rare, dark purple-flowered phenotype) and *D. pauciflora* have been lost as open native vegetation was replaced by dense *Acacia* shrubs (A. Fleischmann and E. Green pers. obs.), and other populations of these species are under threat (Fig. 7).

It should be noted that, in some instances, CPs have been introduced into and become naturalised in areas where they were not previously native. Paradoxically, though often necessarily, this has resulted in the need for eradication programs aimed at controlling introduced populations of species that are at risk of extinction in their natural ranges. For example, extensive introduced populations of *Aldrovanda vesiculosa* have become naturalised in the northeast United States (Cross, 2012a; Lamont et al., 2013; Floyd et al., 2015), including one harbouring tens of millions of individuals, potentially representing the largest population of this species remaining anywhere in the world (Cross et al., 2015, 2016). *Aldrovanda vesiculosa* is recorded from the fossil record in North America but is not considered native to the New World, and although the species appears to compete poorly with native macrophytes and co-occurs with native *Utricularia*, its impact on local ecosystems (particularly aquatic invertebrate communities) remains unknown (Cross et al., 2015).

The North American *Sarracenia*, particularly *S. purpurea* subsp. *purpurea*, has been introduced and naturalised at a number of locations across Europe (e.g., Adlassnig et al., 2010; Walker, 2014), becoming an invasive neophyte at several locations (Walker et al., 2016). Naturalised populations of *Dionaea muscipula* are known from the Apalachicola Forest in Florida (Schnell, 2002) where they were deliberately sown by a local CP grower in the early 1970s (Miller, 2019). Venus Flytraps were also introduced into the Wahner Heide Nature Reserve near Bonn, Germany, where a small population of the threatened *Radiola linoides* (Linaceae) was destroyed by this planting (Fleischmann, 2016) before the introduced species was removed. The Mediterranean *Pinguicula hirtiflora* has been naturalised at two sites in Switzerland and one in the Czech Republic, where it was deliberately planted on a sensitive tufa rock ecosystem (Pyšek et al., 2012), while the European *Pinguicula grandiflora* has become naturalised in protected areas in New Zealand after deliberate plantings, reported in local media under the headline “Rogue carnivorous plant-lovers sabotage National Park” (www.nzflora.info [accessed 2019]).



Fig. 7. Invasive Australian *Acacia* overgrowing open grassland at Kalbaskraal, Western Cape, South Africa, harbouring a dark purple colour variant of *Drosera cistiflora* visible in the foreground. Note the dense, taller understory of grasses under the *Acacia*, resulting from elevated soil [N] (Photo: A. Fleischmann, 2006). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Other examples include the deliberate introduction of the North American *Utricularia inflata* to Germany (Fleischmann, 2016); the introduction of Northern Hemisphere *Drosera rotundifolia* to Patagonia, possibly on soil attached to the boots of a hiker (Vidal-Russell et al., 2019); the naturalisation of the widely cultivated South African species *Drosera aliciae* and *D. capensis* on the Azores (Borges and Costa, 2010; Costa et al., 2013); the introduction of the Western Australian *Drosera pulchella* and *D. × sidjamesii* to a remote island off the coast of New Zealand (T. Krueger via iNaturalist); the introduction of the commonly grown African *Utricularia sandersonii* to the Blue Mountains in New South Wales, Australia (Conn et al., 2004); and, perhaps most notoriously, the introduction of numerous CP species including *Darlingtonia californica*, various *Drosera*, *Heliamphora*, *Sarracenia* (including horticultural hybrids) and *Utricularia* to Albion Bog, a protected Preserve in Mendocino County, northern California, which harbors a unique vegetation of native pygmy pine forest (D'Amato, 1988; Rice, 2008; Gibson, 2018; A. Fleischmann pers. obs.). At this site, the invasive *Drosera capensis* appears to have outcompeted the native *D. rotundifolia*, which is now restricted to only the driest *Sphagnum* cushions where *D. capensis* appears unable to establish (A. Fleischmann pers. obs.). Despite efforts by the Nature Conservancy to remove the introduced plantings from 2008 onwards (Rice, 2008), newly-planted exotic CPs are found every year.

7. Global climatic changes

Global climatic change is a trans-continental issue primarily derived from magnified, temperature-driven hydrological shifts in global aquatic systems which, in turn, affect terrestrial systems mostly through changes in global weather. Research into its predicted effects is increasingly data driven, with sophisticated modelling examining the hydrological impacts (e.g., Gleick, 1986; Shen et al., 2018), economic and food security risks (e.g., Parry et al., 2005; Schmidhuber and Tubiello, 2007), and ecological biodiversity implications (e.g., Dawson et al., 2011) of various climate scenarios and extreme weather events. General consensus suggests that current and projected rates of change in all ecosystems are expected to exert a generally deleterious effect on biodiversity, the integrity and functioning of ecosystems, and individual species survival. Climate change is, particularly outside of equatorial regions, often characterised by observed and predicted warming trends (Huang et al., 2017; Sévellec and Drijfhout, 2018). These trends result in increased severity, frequency, and duration of droughts—anathema to a group of primarily hygrophytic species such as CPs—and an associated increase in fire frequency and severity (as evidenced by the unprecedented ferocity of recent, catastrophic bushfire events in the United States and Australia, where the increased probability of such events and associated ecosystem change is strongly supported by big data; Dutta et al., 2016; Sharples et al., 2016). Generally, wetland ecosystems are considered especially sensitive to climate change (Winter 2007), and evidence suggests aquatic CPs such as *Utricularia intermedia* and *U. ochroleuca* (Adamec, 2018) and *Aldrovanda vesiculosa* (Adamec, 2020) are already being deleteriously affected by changing climate. As such, and given that observations of CP habitat decline made by the authors across many affected regions are consistent with data showing long-term regional and continental decreases in rainfall, many CPs have been—and will likely increasingly be—impacted by climatic change.

The SWAFR is an example of how global climatic change exerts continental and regional shifts in weather, thereby negatively impacting the quality of already imperiled habitat and its component biodiversity. The entire SWAFR is characterised by a distinct geographic gradient in annual rainfall that increases from east to west, and temperatures that increase from south to north (Fletcher et al., 2020). Since records began, and commensurate with anthropogenic climate change in mediterranean regions worldwide, there has been a pronounced decline in precipitation across the SWAFR (Lobell et al., 2011; Hochman et al., 2017), with decreases in annual rainfall of up to 38 mm per decade (Yu and Neil, 1993; Philip and Yu, 2020)

and a ca. 0.9 °C increase in annual average temperatures since 1910 (Lewis and King, 2015). The rainfall decrease has been particularly pronounced during the winter months (i.e. during the growth phase of most CPs from the area) of the past 50 years (Asseng and Pannell, 2013; Philip and Yu, 2020), and has seen a broad westward shift in rainfall zones (Sudmeyer et al., 2016). The movement of these zones may threaten numerous species, but particularly endemics with limited distributions. For example, all six known, extant *Drosera albonotata* populations lie within the 225–450 mm Western Australian Wheatbelt May–October Rainfall Zone (Robinson et al., 2018). However, decreases in rainfall have shifted all the rainfall zones by tens of kilometres (Fig. 8), pushing the eastern boundary of the favourable climate envelope for *D. albonotata* west through half of its known range, likely undermining its fitness to persist in remaining eastern strongholds as a result of the increased probability of more extreme and ultimately fatal droughts.

In an agricultural study examining the quantitative effects of these rainfall shifts on crop production, projected wheat yield potentials shifted an average of 70 km (towards the coast) between the contrasted 1900–1934 and 2000–2016 time periods (Fletcher et al., 2020). While agricultural technology and increased atmospheric carbon dioxide (favouring plant growth) largely mitigate their effects on the actual yields of crops for now, these climatic pressures will challenge the resilience of the unprotected native flora and, with remaining habitat being so highly fragmented, outward migration (a typically gradual process already undermined by the sheer rate of climatic change) of affected species commensurate with shifting favourable climate envelopes becomes impossible. With rainfall levels projected to continue to decline (Pittock et al., 2003), the easternmost natural ecosystems occupied by *D. albonotata* and other co-occurring endemic species may not represent viable refugia in the long term unless actions are taken to reverse habitat fragmentation.

Large portions of the SWAFL were affected by a record to near-record drought period between March and June 2019 (Bureau of Meteorology, 2019). Observations throughout that year indicated that this drought caused prolonged damage to numerous CP populations (T. Krueger pers. obs. 2019–2020; Fig. 9c,d). For example, many dead individuals of the CR *Byblis gigantea* and the VU *B. lamellata* were observed at the last remaining sites of these species (Fig. 9e). Those individuals did not recover throughout the year or during 2020. Very similar observations have also been made for several pygmy *Drosera* species such as *D. omissa* and *D. silvicola*, the latter of which suffered a population decline of ca. 90% at its type locality (T. Krueger pers. obs. 2019). In some tuberous species, such as *D. orbiculata* (VU), almost all flowers were observed to wither before anthesis, resulting in near-zero seed production that year.

Warming trends are also documented near the equator, although the effects on rainfall are less easy to generalise as different regions have experienced decreased annual rainfall, increased annual rainfall or, in some cases, unchanged mean annual rainfall but with significant changes in its seasonality (i.e. pronounced droughts interspersed with extreme and sometimes dangerous rainfall events; Anyah and Qiu, 2012; Diem et al., 2014; Tang, 2019). How such changes affect CPs in their natural environments would likely depend on overall temperature trends, the severity of individual extreme weather events, the intrinsic resilience of the species and ecosystems in question and, to some extent, the ability of affected species to migrate towards more suitable climate envelopes over time. The threat posed by warming trends to species restricted to mountain summits, which includes numerous range-restricted and threatened CPs, is very real; for example, models of global warming-related loss of biodiversity on the tepuis of the Guiana Shield (northeast South America), to which *Heliamphora* is endemic, predicted 80% of the vascular flora (ca. 1700 species) were threatened with extinction. Of these, 400 were tepui endemics representing approximately 50% of all known tepui–endemic species (Nogué et al., 2009; Rull et al., 2019).

Extreme climatic or weather events, whether stochastic or periodic, such as El Niño which causes exceptional drought in the Southeast Asian wet tropics (Ropelewski and Halpert, 1987), represent a severe temporal threat to plants adapted to perhumid conditions such as *Nepenthes* (Steiner, 2002; A. Robinson, pers. obs.). In Southeast Asia, the 1997–98 El Niño event, which saw widespread drought across the region, was one of the strongest on record (Trenberth et al., 2002). Major dieback of *Nepenthes* in Bornean cloud-forest habitat, and significant rates of mortality especially in populations of the large-growing *N. lowii*, was directly observed in August 1998 on Mts. Kinabalu, Mulu and Trus Madi (A. Robinson, pers. obs.). While regeneration of some rapid-growing species to pre-El Niño conditions has since occurred, return climbs to the same peaks in 2002, 2005 and 2007 found that the process of recovery was particularly slow for the large, woodier montane *Nepenthes* (A. Robinson, pers. obs.). Steiner (2002) similarly reports withering of all individuals of a large roadside population of *N. zakriana* [as '*N. fusca*'] in 1999 following the 1997–98 El Niño, from which he found only a single plant recovered in 2000. Long-term projections for northern Borneo suggest that rainfall seasonality may become markedly pronounced, with dry seasons on Mt. Trus Madi, for example, expected to be 20% drier than current (Maycock et al., 2011). Continuing climate shifts will have detrimental effects on *Nepenthes* species restricted to higher elevations, especially owing to their narrower niche tolerance and the dramatic reduction in potentially suitable habitat through habitat clearing (Schwallier et al., 2016).

The Cape Floristic Region (CFR) of South Africa experienced exceptional droughts in the years 2015–2017, three consecutive years with below average rainfall in winter (e.g., Archer et al., 2019, Fig. 9a, b). The CFR is home to 20 species of CPs, 15 of them endemics (including the two species of the Cape-endemic family Roridulaceae; Cross et al., 2018b; Fleischmann et al., 2018). Bioclimatic models predict a massive loss of fynbos in the CFR by 2050 due to global climate change (Midgley et al., 2003). For the Cederberg mountains, where populations of *Roridula dentata* occur, the effects the 2003–2004 drought on the local vegetation have been analysed by Burman (2005) who noted this extreme drought event was considered a “1:100-year occurrence, [that] could be commonplace”. It was followed in that region by the even more severe 2015–2017 drought, clearly at a much faster interval than anticipated. Burman (2005) noticed that the drought impacts on the local vegetation were not uniform, and that plant mortality rate depended on soil type and elevation; these observations were supported by

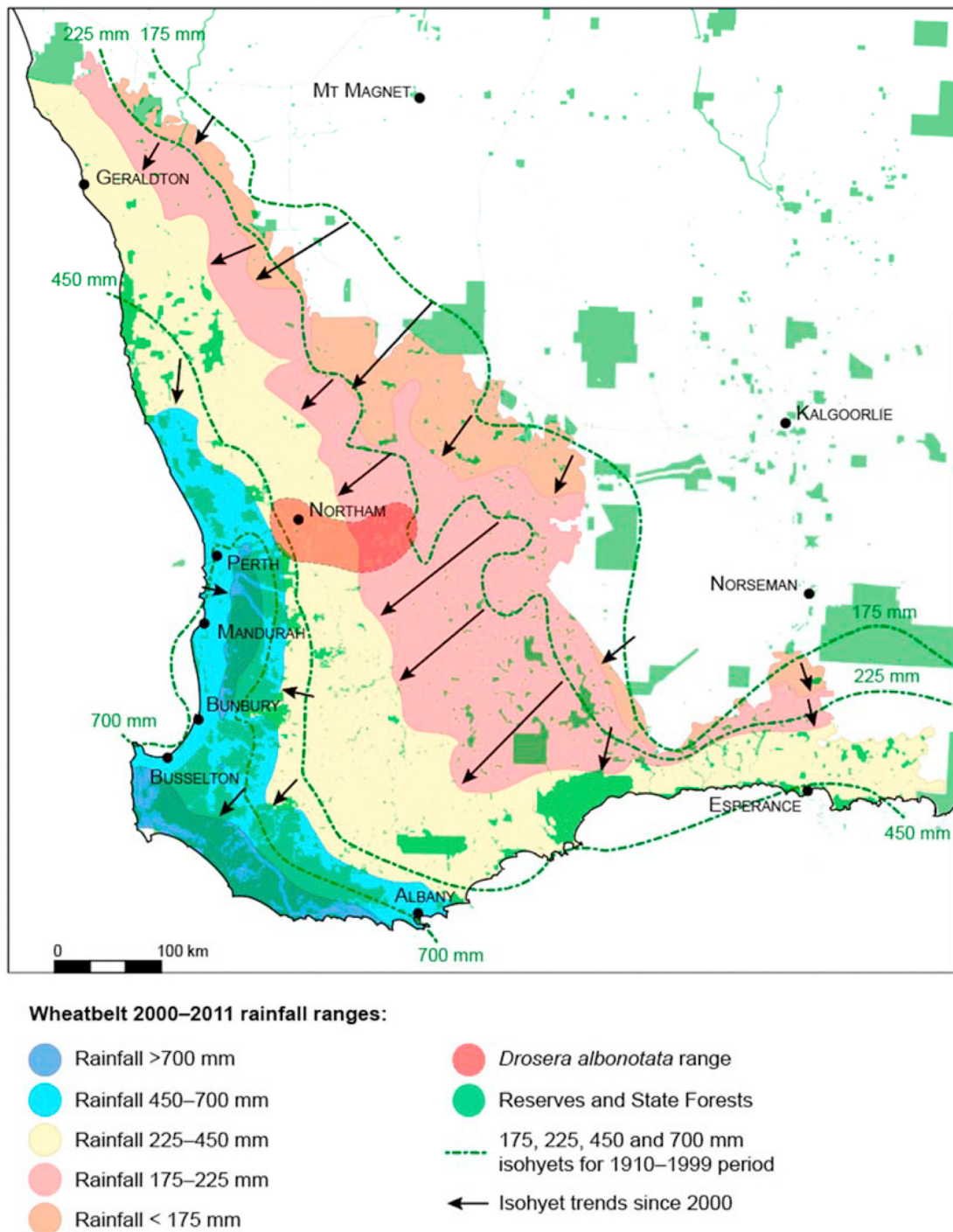


Fig. 8. A map of Western Australia's Wheatbelt Region with 2000–2011 rainfall ranges indicated, along with isohyets demonstrating the boundaries for average rainfall amounts in the 1910–1999 period. The approximate range of *Drosera albonotata* from Robinson et al. (2018) is indicated and the Reserves and State Forests of Western Australia are superimposed to illustrate the extreme habitat loss and fragmentation of native vegetation across the region (Illustration: A. Robinson, adapted from maps provided by the Western Australian Agriculture Authority, 2014, and Geographic Information Services, 2016).

experiments (Born and Linder, 2018) showing that soil drainage characteristics, but not plant-specific drought-tolerance, largely explained the distribution of the Cape flora.

In the Mediterranean Basin, climate change is causing stronger seasonality with longer, drier and hotter summers (e.g., Li et al., 2013), and exceptional droughts from persistent summer heat waves have caused severe population declines in some

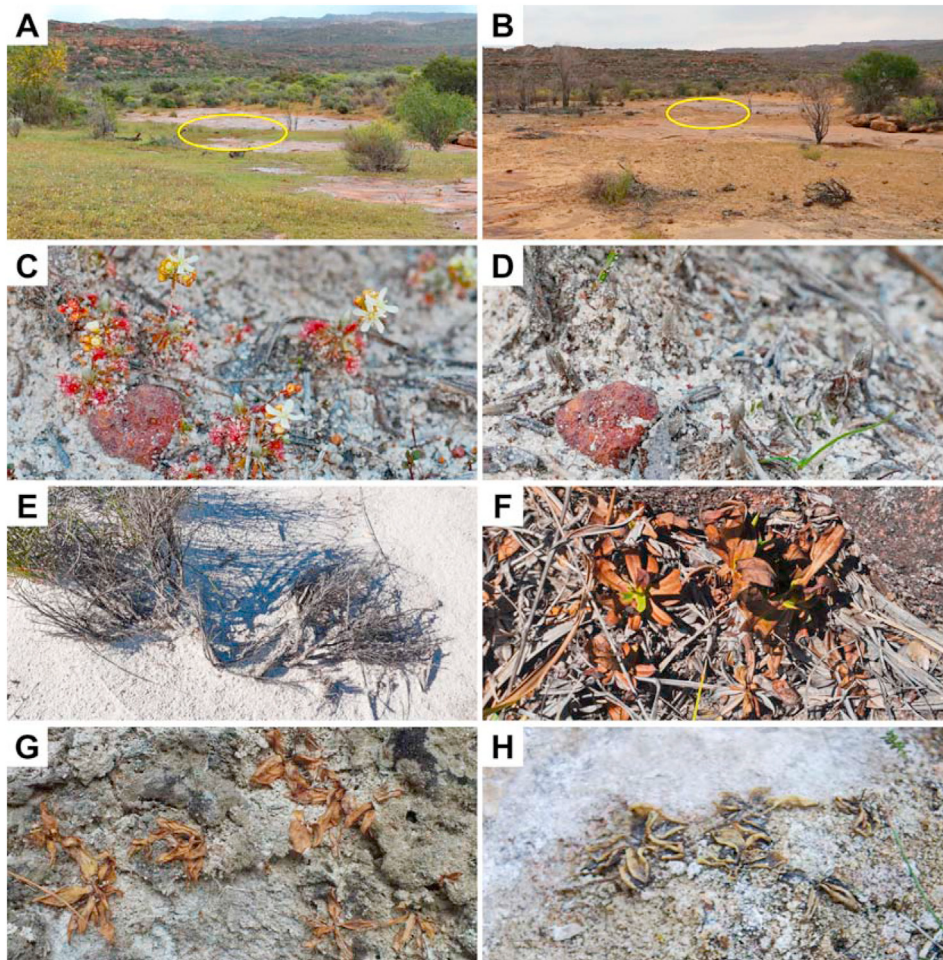


Fig. 9. Examples of the effects of intense and prolonged drought on carnivorous plants. **A.** Habitat of the winter-growing geophytic NT *Drosera alba* (population marked in yellow) on Gifberg, Western Cape Province, South Africa during a normal winter rainfall season in 2014 (Photo: C. Dietz). **B.** The same population of *D. alba* following an exceptionally dry winter rainfall season in 2019, which resulted in mortality of all individuals (Photo: C. Dietz). **C.** Type location of the CR *Drosera leioblastus* in Western Australia, at which ca. 20 individuals were located in September 2019 (Photo: T. Krueger). **D.** The same population of *D. leioblastus* in late July 2020 following severe drought, which resulted in mortality of all individuals (Photo: T. Krueger). **E.** Prolonged drought conditions in 2019–2020 resulted in population declines of up to 50% for the VU *Byblis lamellata* near Eneabba, Western Australia, with mortality observed in numerous established individuals such as the large plant pictured (Photo: T. Krueger). **F.** Drought-affected *Nepenthes pervillei* individuals on Mahé, Seychelles, following exceptionally dry conditions in early 2012 (Photo: T. Krueger). **G.** Dead individuals of the locally-endemic CR *Pinguicula mariae* on a dry limestone seepage in Trombacco, Apuan Alps, Italy, following an extremely hot and dry summer in 2017 (Photo: Giulio Pandeli). **H.** Dead rosettes of the VU *P. sehuensis* in Sardinia, Italy, on a limestone seepage that dried out during the particularly hot and dry Mediterranean summer in 2017 (Photo: Marcello Cannas). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Mediterranean *Pinguicula* in the past decade, predominantly of lowland species at colline or montane elevations. Their habitats on seepage sites or wet dripping walls are dependent on constant water supplies, the sources of which are usually situated upslope towards the mountain tops and fed by frequent winter rains and periodic torrential summer rains. During recent, exceptionally hot, long and dry summers, several low-elevation seepage habitats have become fully desiccated, especially dripping walls on calcareous rock, leading to the death of all lithophytic hygrophytic plant communities. This caused a severe decline in known populations and localities of *P. mariae*, a lowland species endemic to the Apuan Alps of Italy (G. Pandeli and M. Saroldi, pers. comms. 2017; Fig. 9G). Similar impacts were observed for low-elevation populations of *P. hirtiflora* in Italy following the long and exceptionally dry summer of 2017 (A. Izzo and M. Saroldi, pers. comm. 2017, 2019). The recently described VU *P. sehuensis*, a micro-endemic species from Sardinia, Italy, known only from eight small populations discovered in 2014 (Bacchetta et al., 2014), suffered from a population decline of ca. 80% following two exceptional droughts during the summers 2017 and 2018. Only 13% of all known plants survived the drought in 2017, the rest succumbed (G. Bacchetta and M. Saroldi, pers. comms. 2017; Fig. 9H). Climate change is demonstrably threatening some of the narrowly endemic Mediterranean species of *Pinguicula*, several of which are already endangered because of their very small population sizes (Fois et al., 2017; Fleischmann and Rocca, 2018).

The Brazilian *campos rupestres* harbours a great diversity of CPs—at least 70 species (Gonella and Baleeiro 2018)—and is, according to predictive models, on a course towards ecological collapse on account of climate change, amounting to a loss of up to 82% of its suitable area by 2070 (Fernandes et al., 2018). The scenario is especially concerning for species restricted to single mountain-top localities, such as the CR *Drosera graminifolia* (Gonella et al., 2012), CR *D. magnifica* (Gonella et al., 2015), VU *Genlisea exhibitionista*, and NT *Genlisea uncinata* (Fleischmann et al., 2011), as these species are effectively incapable of upward migration to more suitable climate envelopes and therefore at greater risk of extinction. Projections also point to severe contractions of climate-suitable areas by 2080 in the northern portion of the Espinhaço Range, with the likely extinction of several endemics (Bitencourt et al., 2016) which, in this area, would include several range-restricted species of *Drosera*, *Utricularia*, *Genlisea* and *Philcoxia* (Taylor et al., 2000; Fleischmann et al., 2011; Carvalho and Queiroz, 2014; Gonella et al., 2014).

CPs may also be affected in the long-term by phenological changes caused by global climatic change, such as seasonal shifts of budding, hibernation and anthesis, or plant-pollinator mismatches (Richardson et al., 2013; Gérard et al., 2020). Several CP species have specialist pollinators, for example the bird-pollinated *Utricularia menziesii*, *U. campbelliana*, *Pinguicula hemiepiphytica* and *P. laeueana* (Lampard et al., 2016; Plachno et al., 2019) and some populations of *D. cistiflora* (Cross et al., 2018b; von Witt et al., 2020), and the role of potential seasonal shifts in prey abundance and composition (and the influence of this on prey spectra) remains unclear (Krueger et al., 2020). Insect population sizes and diversity are known to be markedly affected by climatic events (Boggs, 2016; Wagner, 2020), and the effects of species turnover caused by global climatic change may present additional impacts to CP species and their habitats.

8. Poaching and botanical tourism

The illegal collection (poaching) of CPs from wild habitats to supply hobby cultivation markets is a significant and growing threat to many species, despite such activity being a criminal offence in most jurisdictions around the world. The ecological novelty of CPs makes them extremely horticulturally-desirable, and there is a large international community of CP enthusiasts. Sadly, it is the horticultural enthusiasm of this group that provides a market for—and is the only driver of—illegal collection. Clarke et al. (2018) note that, “growers who believe that their right to collect and grow carnivorous plants outweighs the rights of the plants to persist unmolested in the wild continue to drive strong demands for wild-collected plants of desirable species.” Indeed, the demand particularly for rare or morphologically-unique species or individuals is high, as evidenced by frequent requests for material in various online forums and on social media. It is common for requests seeking seeds or plants of such species to be directed at the authors or photographers within days or even hours of discoveries being documented (this has occurred to all authors of the present work), and in some instances entire populations have been poached within days of their discovery (Rice, 2003). While a growing number of CP species can be easily and sustainably obtained from commercial nurseries around the world, many collectors demand “clones” of wild origin, accompanied by known locality data (Meyers-Rice, 1996, 2001). Although CPs are no longer illegally collected to satisfy the demand of garden centres, plant markets and commercial business (as was once the case for *Dionaea* and *Sarracenia* in the United States; D’Amato, 2013), widespread poaching by unscrupulous individuals remains an open, tolerated secret in the international CP community. Given that the collection of native flora for commercial purposes in countries harbouring many commonly-cultivated CPs such as Australia, Brazil, Malaysia, and the United States is tightly regulated, it is probable that the majority of species from those countries introduced to cultivation in recent decades originate from illegally-collected material.

Illegal collection for horticultural trade remains a significant threat to *Dionaea muscipula* and *Sarracenia* (Meyers-Rice, 2001; Clarke et al., 2018), and is the principal threat to the CR *Sarracenia oreophila* and EN *S. alabamensis* and *S. jonesii* (Meyers-Rice, 2001). The impacts of poaching on *Cephalotus follicularis* have been significant, with well-known populations almost entirely extirpated by illegal collection and local government land managers reporting shovel holes where individuals had previously been (Cross et al., 2019). Illegal collection is reported as a threat to numerous species of *Drosera*, *Heliamphora*, *Pinguicula*, *Triphyophyllum*, and even *Utricularia* (Appendix S1). However, our analyses clearly indicate that the genus most significantly impacted upon by poaching is *Nepenthes*. The high variability in pitcher colour and morphology, even within species, has generated a strong market for *Nepenthes* in horticulture (Simpson, 1995; Phillipps and Lamb, 1995). Illegal collection has dramatically impacted populations of many *Nepenthes* species (Clarke et al., 2018), and appears to have increased in recent years, concomitant with both an increase in botanical tourism to regions where *Nepenthes* occur and a higher international profile for the genus in horticulture. Poaching now threatens 45 species of *Nepenthes* (almost one-third of all species in the genus), including 13 that are CR, five that are EN, and seven that are VU, and is the only recognised threat to 27 species. Poaching has been identified as a threat to *Nepenthes* from Cambodia (Mey et al., 2010), Malaysian Borneo (Wulffraat and Morrison, 2013; Bukhori et al., 2018), Indonesia (McPherson, 2009; Cheek et al., 2018), and the Philippines (Robinson et al., 2009; Lagunday and Amoroso, 2019), most notably for CR species including *N. clipeata*, *N. jacquelineae*, *N. pitopangii*, *N. rigidifolia*, *N. tenuis* and *N. undulatifolia*. Paradoxically, *Nepenthes* have been identified as potential flagship tourism species in countries such as Indonesia where the impacts of poaching on this genus are most severe (Setiawan, 2017).

Poached plants, particularly of *Nepenthes*, are commonly advertised openly on online marketplaces and on social media, often with no effort made to mask their wild-collected origin (A. Fleischmann, A. Robinson, A.T. Cross, T. Krueger, P. Gonella pers. obs.). Unless there is a paradigm shift in the attitude and actions of the international community of CP growers and collectors to actively and immediately close down the market for illegally-collected wild plants, coupled with greater regulatory enforcement in regions where illegal collection is most significant, many of the most iconic and celebrated CP species

will likely be driven to extinction within coming years. Through inaction, the international CP community would be complicit in these extinctions.

9. Future conservation actions and priorities

Insufficient data relating to the distribution, abundance and ecology of plant species has resulted in a great number of DD rated taxa in IUCN Red List classifications, especially in highly-diverse groups and in endemism-rich regions (Troudet et al., 2017; Hochkirch et al., 2020). Indeed, data deficiency is one of the largest problems hindering international biodiversity assessments and conservation programs (Hochkirch et al., 2020). The relatively low number of CP species recognised as DD (11.2%; Fig. 1) reflects the high research interest afforded this group compared with many other plants, and the group-wide effort to undertake conservation assessment presented in this manuscript. However, taxonomic or geographic bias towards small, well-studied groups and regions is common in IUCN Red List data (Troudet et al., 2017), and is evident for CPs when considering the two largest genera *Drosera* and *Utricularia*. Although these genera both equally contain 248 accepted species, with species from each commonly occurring sympatrically and therefore likely to be impacted upon by the same threats, only 3% of *Drosera* are assessed as DD (and 23% as CR, EN, VU or NT) while 16% of *Utricularia* are assessed as DD (and 9% as CR, EN, VU or NT). *Utricularia* is less well-studied than *Drosera*, particularly taxonomically (A. Fleischmann and P.M. Gonella pers. obs.), as most species are difficult to differentiate and identify when not in flower. As such, it appears likely that the number of threatened species in *Utricularia* is underestimated.

Taxonomic resolution plays a significant role in conservation classification. Review of the literature in the present study found numerous historical IUCN Red List assessments to be outdated and requiring revision, commonly because new species classifications/circumscriptions made a change of conservation status category necessary. For example, a return to the remote type locality of *Nepenthes fusca* after a period of 93 years revealed that the name *N. fusca* s.lat. incorporated several distinctive species with very different population sizes and threat dimensions, revising the previously circumscribed widely-distributed NT *N. fusca* into three geographically-separated species with different conservation status categories (Robinson et al., 2019a). Recently-described (and undescribed) species are more likely to exhibit range restriction and be at risk from threatening processes, and are thus more likely to have a higher probability of extinction (Scheffers et al., 2012). Examples for CPs recognised after January 2020 (and thus not included in analyses in the present study) which meet these criteria are *Drosera buubugujin* (CR; two populations known; Mathieson and Thompson, 2020), *D. stipularis* (not evaluated; two populations known; Baleeiro et al., 2020), *D. arachnoides* (VU; 4–5 populations known; Fleischmann et al., 2020), *Nepenthes maximoides* (CR/EX?; one historic collection; King and Cheek, 2020), *Pinguicula bustamanta* (not evaluated, one population known; Zamudio and Nevárez-de los Reyes, 2020), *P. rosariae* (DD, three collections; Casper et al., 2020), *Utricularia speciosa* (VU; four populations known; Jobson and Baleeiro, 2020), and *U. dichotoma* subsp. *novae-angliae* (VU, six populations known; Jobson and Baleeiro, 2020). This reinforces the importance of conserving remaining natural vegetation, as most undiscovered biodiversity is presumed to exist in known biodiversity hotspots (Joppa et al., 2011). A considerable proportion of species are likely to become, or have already become, extinct before even being described (Tedesco et al., 2014).

Most CP species and genera are pioneers of freshly-exposed oligotrophic wet soils (Brewer and Schlauer, 2018), and most produce large quantities of small seeds to rapidly colonise new habitats (R-strategy; Cross et al., 2018b). Thus, while suitable habitat remains and natural ecological processes can be maintained, there is hope for CPs to survive (in) the Anthropocene. Initiatives conserving remnant habitat and restoring degraded habitat (i.e., *in situ* conservation) must be a primary focus. It is unlikely that “*ex situ*” conservation (see IUCN/SSC, 2014), in the form of maintaining more or less randomly-selected gene-pools by growing threatened species under axenic conditions or in cultivation, will assist the long-term survival of species threatened with extinction. Conservation without consideration of the integrity of natural systems is nonsensical (Braverman, 2014), as if suitable habitat is lost, ecosystem functioning is compromised, or the abundance or occurrence of prey or biological symbionts is greatly reduced, species reintroductions will not be successful (e.g., Maschinski and Haskins, 2012). The only successful reintroductions of CPs to natural habitats from cultivated material known to the authors of the present work are those of autochthonous, extinct-in-the-wild *Aldrovanda vesiculosa* in Japan (Kondo et al., 1997; Cross, 2012a).

A number of *in situ* conservation programmes are in place for threatened CPs, including for *Sarracenia* in the United States (Rice, 2008; Ziemer, 2010), and flag-ship projects such as the *Nepenthes clipeata ex situ* conservation project (Cantley et al., 2005) and the Ark of Life project (van den Broek, 2015). However, maintaining *ex situ* populations of threatened species under autecologically optimised conditions may not necessarily conserve the same gene pool that is adapted to the syn-ecological optimum, and risks artificially selecting for genotypes and traits that may be deleterious under natural conditions. Even the most well-planned *ex situ* conservation programs are not guaranteed to successfully re-establish wild populations (Braverman, 2014). Additionally, promotion of *ex situ* conservation (especially community-driven projects) for species of high horticultural value may also have the unintended consequence of creating greater demand for wild-collected plants, with individuals collecting threatened species under the misguided perception of “saving them” from extinction in natural habitats. This risk is greatest for *Nepenthes*, as *ex situ* conservation is considered a realistic goal for threatened species in this genus (Simpson, 1995; Cantley et al., 2005; Ziemer, 2010) despite numerous species having already been driven almost to extinction by illegal wild-collection.

10. Recommendations and conclusions

We provide the following ten recommendations from the results of our systematic re-examination of the conservation status and threats to CPs globally:

- Urgent global action is required to reduce rates of habitat loss and land use change, particularly in already highly-cleared regions harbouring high CP biodiversity and numerous threatened CP species such as the SWAFR, Brazil, southeast Asia and the United States;
- Stronger focus should be placed upon the preservation and protection of remnant CP habitats around the world, particularly areas harbouring high CP diversity and/or threatened CP species, concomitantly through the expansion of existing reserves and the establishment of new conservation estates;
- Efforts should be made to elucidate the distribution and threats faced by species currently assessed as DD, through targeted surveys and ecological study;
- Populations of threatened CP species occurring on privately-owned land in countries such as the United States must be afforded better legal protection;
- Better and more consistent enforcement of environmental protection laws is required, especially within conservation areas and in ecosystems harbouring threatened CP species, particularly in countries such as Brazil, the United States, Indonesia and the Philippines;
- Environmental impact assessments must adequately consider biodiversity, and improved education is required to ensure that industry, governments and communities better understand the importance of, and human reliance upon, biodiversity and ecological functioning (e.g., [Breed et al., 2020](#));
- Conservation activities should prioritise invasive species management, protection of CP-associated biological mutualists, and the maintenance and preservation of natural ecosystem processes such as fire regimes and hydrological functioning. Ecological restoration initiatives should seek to reinstate these natural processes in degraded landscapes where ecosystem functioning has been impaired;
- Fire management activities, where necessary, should be evidence-based and carefully undertaken to ensure they do not deleteriously affect species with idiosyncratic fire responses and requirements. Any fire management should be underpinned by empirical understanding of how different species respond to fire regimes and are influenced by the timing and spatial arrangement of fires ([Bradshaw et al., 2018](#));
- There must be immediate and concerted global action to close down the market for illegally-collected wild plants, coupled with greater regulatory enforcement of biodiversity protection laws, to expediently end the poaching of CPs;
- Future research should assess the apparently limited effectiveness of some *ex situ* CP conservation initiatives in meaningfully contributing to translocation programmes or demand-reduction initiatives, and explore how these activities might better complement *in situ* efforts to conserve and restore remnant and degraded natural habitats.

Many CPs face imminent extinction, and conservation initiatives must be established immediately to prevent these species being lost in coming years and decades. We must dramatically reduce the rate at which natural vegetation around the world is being cleared and degraded, particularly in CP biodiversity hotspots including the SWAFR, Southeast Asia, south-eastern United States, and Brazil, and increase efforts to reinstate native vegetation through activities such as ecological restoration. Much greater focus must be placed upon the preservation and maintenance of natural ecological processes such as hydrological functioning and fire, and on the restoration of these processes in landscapes where they have been degraded or altered. Crucially, and yet perhaps most easily achieved of the actions required, concerted international efforts led by high-profile CP groups such as the International Carnivorous Plant Society and the CPSG must immediately focus on eradicating poaching and ensuring that all horticultural trade in these species is ethical, sustainable, regulated, and transparent. Without urgent action, we stand to lose some of the most ecologically unique, evolutionary interesting, and horticulturally-celebrated species on the planet.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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