A review of the conservation threats to carnivorous plants

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Abstract

Over half of the carnivorous plant species assessed by the International Union for the Conservation of Nature (IUCN) are listed as threatened (i.e. vulnerable, endangered, or critically endangered), but the threats to carnivorous plants have not previously been quantified systematically. In this review, we quantify the conservation threats to carnivorous plant taxa worldwide. Using the IUCN Red List, a literature search of Web of Knowledge, and the National Red Lists database, we collected data on the threats to 48 species of carnivorous plants from nine genera. The most common threat was habitat loss from agriculture, followed by the collection of wild plants, pollution, and natural systems modifications. A principal coordinate analysis revealed that species within a genus often faced similar threats, and an indicator species analysis found positive associations among species in the genus Sarracenia and agricultural activities, over-collection, invasive species, and pollution. Future research should further quantify the effects of pollution on carnivorous plants, and more thoroughly examine the potential role of carnivorous plants as indicator species for wetland health. More research is also needed to quantify the extinction risk for many carnivorous plants, as presently only around 17% of species have been assessed by the IUCN. Ensuring the conservation of carnivorous plants will help maintain the important ecosystem services they provide and prevent secondary extinctions of specialist species that rely on them.

Keywords:
- Carnivorous plants
- Conservation
- Habitat loss
- Invasive species
- Over-collection
- Pollution

1. Introduction

Identifying the conservation threats for taxa can have important management implications. For example, they can guide policy makers to prioritize certain areas of conservation when limited funding is available (Hughey et al., 2003), and also can be used to implement precautionary conservation measures for species which threats have not been directly assessed. While the conservation threats for different groups of mammals (Hayward, 2009), birds (Feeley and Terborgh, 2008), reptiles (Filippi and Luiselli, 2000), and amphibians (Stuart et al., 2004) have been quantified both regionally and globally, less attention has been accorded to other groups, such as flowering plants. Furthermore, of the...
approximately 268,000 known species of angiosperms, only about 3% have been evaluated by the International Union for the Conservation of Nature (IUCN) (2010). However, of the relatively small number of angiosperm species that have been evaluated, 70% are listed as threatened (i.e. vulnerable, endangered, or critically endangered) (IUCN, 2010). One such group of angiosperms for which many species are thought to be imperiled are the carnivorous plants (Schnell, 2002).

There presently are around 600 described species of carnivorous plants from 17 genera (Ellison and Gotelli, 2009), with new species frequently being described (Cheek and Jebb, 2009; Clarke et al., 2003; Clarke and Kruger, 2006; Mann, 2007). Of the 102 carnivorous plant species (from seven genera) that have been evaluated by the IUCN, seven are listed as critically endangered, 11 are listed as endangered, and 39 are listed as vulnerable (IUCN, 2010). Consequently, of these IUCN-evaluated species, 56% are considered to be threatened. Although lower than the value for angiosperms as a whole (70%), 56% is still higher than the value for all taxa (33%), or for any evaluated vertebrate group (IUCN, 2010). While there have been several species-specific studies regarding carnivorous plant conservation threats, and their threats as a group are often alluded to (Schnell, 2002), threats to carnivorous plants have not previously been quantified in any systematic way. In this review, we provide a quantitative description of the conservation threats to carnivorous plant taxa worldwide.

1.1. Evolution and ecology of carnivorous plants

Carnivorous plants have arisen from at least six distinct lineages, all having evolved modified leaves specialized for capturing animals (predominantly arthropods) and many having this prey to acquire nutrients (Albert et al., 1992; Bayer et al., 1996; Cameron et al., 2002; Ellison and Gotelli, 2009; Juniper et al., 1989; Rivadavia et al., 2003). Utilizing animals as prey is thought to be an adaptation that carnivorous plants have for living in moist, nutrient-poor soils (Juniper et al., 1989). Carnivorous plants generally are poor competitors for light and nutrients with non-carnivorous plant species, and therefore the terrestrial species often require fire to reduce the intensity of competition (Brewer, 2001, 2003; Folkerts, 1982; Juniper et al., 1989; Kesler et al., 2008). While in temperate regions most carnivorous plants are found in bog and fen habitats, in tropical and subtropical regions some species also inhabit forested areas with drier soils and greater shade (Juniper et al., 1989). It is through all of these regions, that habitats for carnivorous plants are threatened by various factors such as agriculture, deforestation, drainage, eutrophication, and fire suppression (Brinson and Malvarez, 2002; Folkerts, 1982; Gardner et al., 2010; Moore, 2002; Sodhi et al., 2010; van Diggelen et al., 2006).

Conserving carnivorous plants could also benefit many other taxa. Carnivorous plants often have surprising and sometimes complex interactions with animals aside from obtaining nutrients from them (Clarke et al., 2009; Jennings et al., 2010; Moon et al., 2010; Zamora and Gomez, 1996), in some cases forming what are thought to be obligate mutualisms (Anderson and Midgley, 2002). For example, pitcher plants are arguably foundation species (Ellison et al., 2005), providing habitat for entire communities of specialists that completely rely on pitcher plants for their existence (Buckley et al., 2010; Rymal and Folkerts, 1982). Some species of pitcher plant can even act as refugia for certain amphibians (Das and Haas, 2010; Russell, 2008). Hence, the loss of carnivorous plants could result in secondary extirpations and extinctions.

Carnivorous plants also seem to provide humans with various ecosystem services. For instance, carnivorous plants consume large quantities of dipterans (Ellison and Gotelli, 2009). Many dipterans, such as mosquitoes, midges, deerflies, and horseflies, are human pests that can transmit human diseases. In addition, the aquatic carnivorous plant genus, Utricularia, consumes mosquito eggs and larvae (Angerilli and Beirne 1974; Juniper et al., 1989), and even regularly depredates human schistosome miracidia and cercariae (Gibson and Warren, 1970). Human schistosomes infect more than 207 million people worldwide, more than 700 million are at risk, and approximately 20 million suffer severe consequences annually (Steinmann et al., 2006). Hence, there is considerable evidence that carnivorous plants reduce human bites from insect pests and perhaps even diminish human disease risk. Consequently, the conservation of carnivorous plants could benefit humans.

2. Material and methods

2.1. Data collection

We used three methods to obtain data on threats to carnivorous plants. First, we searched the IUCN Red List database (www.iucnredlist.org) on 5 August 2010 for the presence of all carnivorous plant genera (Aldrovanda, Brocchinia, Byblis, Catopsis, Cephalotus, Darlingtonia, Dionaea, Drosera, Drosophyllum, Genlisea, Heliamphora, Nepenthes, Pinguicula, Roridula, Sarracenia, Triphyophyllum, and Utricularia). Second, on 10 August 2010 we conducted a search using Web of Knowledge (www.isiknowledge.com) to identify relevant peer-reviewed literature considering the threats to carnivorous plants, using ‘carnivorous plants’, ‘conservation’, ‘threats’, and each genus name as key words. As we limited our search to peer-reviewed literature, we included both empirical and observational studies that provided an abstract in English. Third, we searched the National Red List database (www.nationalredlist.org) on 7 January 2011 for the presence of all carnivorous plant genera. Once the relevant literature was obtained, we classified any documented threats following the unified scheme proposed by Salafsky et al. (2008). In this scheme there are three hierarchical levels of threats which increase in specificity with each level. For example, there are 11 1st level categories, consisting of: (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. After threats are assigned to this 1st level, there are further 2nd level categories (between three and six for each 1st level category) into which they can be classified (Salafsky et al., 2008).

2.2. Data analysis

We conducted a principal coordinate analysis (PCoA) based on Jaccard’s distance to determine the relationship among threat categories, among carnivorous plant species, and between threat categories and species. The analysis was conducted on a matrix that described whether or not there was any evidence that a species was impacted by each of the 11 1st level threats. The ordination analysis was conducted using CANOCO 4.5 (ter Braak and Smilauer, 2002) and the biplot was created using CanoDraw 4.12 to display the ordination results (ter Braak and Smilauer, 2002). The scores were post-transformed so that correlations of the species and threat categories with the ordination axes could be inferred by perpendicular projection.

To determine which taxa-threat associations were greater than expected by chance, we conducted an “indicator species analysis” in PC-ORD v. 5.01 (McCune and Mefford, 1999), which follows the general guidelines of Dufrene and Legendre (1997). This analysis was conducted at the genus level given that we did not have
replication at the species level and that species within a genus tended to have similar threats (Fig. 2). We conducted the analyses on genera with five or more species in the database (Drosera, Nepenthes, Pinguicula, Sarracenia, and Utricularia) and used Monte Carlo permutation tests to evaluate the significance of the association for each genus, reassigning the sample units to the 11 threat categories 4999 times.

### 3. Results

We found data on the threats to 48 species of carnivorous plant (Table 1). The data available spanned nine genera of different growth forms (Aldrovanda, Darlingtonia, Dionaea, Drosera, Drosophyllum, Nepenthes, Pinguicula, Sarracenia, and Utricularia) and covered six continents (Africa, Asia, Australia, Europe, North America, and South America). The number of species with documented threats by continent was highly variable, with threats found for 19 species in North America, 15 species in Asia, seven species in Europe, six species in South America, two species in Africa, and one species in Australia (we found threats for two species on multiple continents). All 11 of the 1st level threat categories proposed by Salafsky et al. (2008) were documented as affecting carnivorous plants, as were 17 2nd level categories. However, 2nd level threats were not equally distributed among all 1st level threats, with some 1st level threats, such as natural system modifications, having three 2nd level threats (fire and fire suppression, dams and water management/use, and other ecosystem modifications), while others, such as geological events, only had one 2nd level threat (avalanches/landslides). Mean number of 2nd level threats per species was 2.9 (range = 1–8), with one species, the green pitcher plant (Sarracenia oreophila), facing eight 2nd level threats. The most common 1st level threats were agriculture and aquaculture, biological resource use, pollution, and natural systems modifications, (7) invasive and other problematic species and genes, (9) pollution, (10) geological events, and (11) climate change and severe weather.

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>1st level threat category</th>
<th>Reference(s)</th>
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</thead>
<tbody>
<tr>
<td>Aldrovanda vesiculosa</td>
<td>x</td>
<td>Adamec (1995, 2005) and Kandu et al. (1996)</td>
</tr>
<tr>
<td>Darlingtonia californica</td>
<td></td>
<td>Folkerts (1977)</td>
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<tr>
<td>Dionaea muscipula</td>
<td>x</td>
<td>Folkerts (1977) and Lukens (2005)</td>
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<tr>
<td>Drosera anglica</td>
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<td>Huntke (2007)</td>
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<td>Drosera brevifolia</td>
<td></td>
<td>Saridakis et al. (2004)</td>
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<tr>
<td>Drosera burmannii</td>
<td>x</td>
<td>Jayaram and Prasad (2006)</td>
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<tr>
<td>Drosera cendeensis</td>
<td></td>
<td>Duno de Stefano and dos Santos Silva (2001)</td>
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<td>Drosera communis</td>
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<td>Saridakis et al. (2004)</td>
</tr>
<tr>
<td>Drosera filiformis</td>
<td></td>
<td>Freedman et al. (1992) and Landry and Cwynar (2005)</td>
</tr>
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<td>Drosera griefei</td>
<td></td>
<td>Lowrie and Marchant (1992)</td>
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<tr>
<td>Drosera indica</td>
<td>x</td>
<td>Jayaram and Prasad (2006)</td>
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<td>Drosera intermedia</td>
<td></td>
<td>Mackun et al. (1994) and Rassi et al. (2001)</td>
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<td>Drosera montana</td>
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<td>Drosera sp.</td>
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<td>Drosera villosa</td>
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<td>Drosophyllum laxitunicum</td>
<td>x</td>
<td>Correia and Freitas (2002) and Garrido et al. (2003)</td>
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<td>Nepenthes alata</td>
<td>x</td>
<td>Simpson (1995)</td>
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<td>Simpson (1995)</td>
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<tr>
<td>Nepenthes bokor</td>
<td>x</td>
<td>Cheek and Jebb (2009)</td>
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<td>Simpson (1995)</td>
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<td>de Belair and Diadema (2008)</td>
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<td>Eysink and De Brujin (1997)</td>
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<td>x</td>
<td>Folkerts (1977)</td>
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<tr>
<td>Sarracenia alabamensis subsp.</td>
<td>x</td>
<td>Folkerts (1977)</td>
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<td>Schnell et al. (2000b)</td>
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<td>Folkerts (1977)</td>
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<td>Folkerts (1990) and Schnell et al. (2000c)</td>
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<td>Sarracenia minor</td>
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<td>Schnell et al. (2000d)</td>
</tr>
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<td>Sarracenia oreophila</td>
<td></td>
<td>Carter et al. (2006), Govus (1987) and Schnell et al. (2000e)</td>
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<td>Sarracenia psittacina</td>
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<td>Schnell et al. (2000f)</td>
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<td>Sarracenia purpurea</td>
<td></td>
<td>Gotelli and Ellison (2002)</td>
</tr>
<tr>
<td>Utricularia fibrosa</td>
<td></td>
<td>Morgan and Philipp (1986)</td>
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<tr>
<td>Utricularia purpurea</td>
<td></td>
<td>Vaithyathan and Richardson (1999)</td>
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<td>Utricularia simulans</td>
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<td>Schnell (1980)</td>
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<td>Utricularia sp.</td>
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<td>David (1996)</td>
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<tr>
<td>Utricularia striatula</td>
<td></td>
<td>Chaturvedi (2005)</td>
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</table>

a 1st level threat categories correspond to the classification proposed by Salafsky et al. (2008): (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.
and pulp plantations and livestock grazing were each threats to
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ious plant species). The threats were fairly evenly distributed
though we found no record of any aquacultural threats to carniv-
habitat loss through the planting of various crops, but also covered
impacts of grazing by animals, and construction of fish hatcheries
sequence of species within a genus having similar threats, some
similar threats (Fig. 2). For instance, Sarracenia species were predomin-
ently affected by over-collection (IV = 32.0, p = 0.012; when excluding
perhaps as a consequence of species within a genus having similar threats, some
threats were also positively correlated, with residential and com-
mercial development, natural systems modifications, invasive
species, and pollution having positive associations (Fig. 2). However,
other threats, such as agriculture and aquaculture and biological
resource use, did not exhibit close relationships with any other
threats.

3.2. Agriculture and aquaculture

The most common 1st level threat to carnivorous plants was from agriculture and aquaculture, which affected a total of 24 spe-
cies (Fig. 1a). Agriculture and aquaculture generally involved direct
habitat loss through the planting of various crops, but also covered
impacts of grazing by animals, and construction of fish hatcheries
(though we found no record of any aquacultural threats to carniv-
orous plant species). The threats were fairly evenly distributed
among three 2nd level categories. Specifically, annual and peren-
nial non-timber crops were a threat to 11 species, while wood
and pulp plantations and livestock grazing were each threats to
10 species (Fig. 1b). Annual and perennial non-timber crop threats
covered species from all genera in the review except Darlingtonia.

3.3. Biological resource use

Biological resource use was the second most common 1st level
threat to carnivorous plants, with 21 species affected (Fig. 1a). This
category covered the collection of wild plants, and other activities
such as logging and wood harvesting that result in direct habitat
loss for carnivorous plants. Collection of plants from the wild
was the most common 2nd level threat category (affecting 19 spe-
cies) (Fig. 1b), and can exert strong negative effects on populations
as collectors often remove larger individuals (Luken, 2005). As
many carnivorous plants are relatively slow to mature, the persist-
tent loss of older individuals can severely impact the population
structure. Collection of wild plants was a particularly common
threat for pitcher plants (Darlingtonia, Sarracenia, and Nepenthes)
and Venus flytraps (Folkerts, 1977, 1990; Luken, 2005), where they
are generally taken to be sold for profit or for private collections.
Additionally, some species, such as Drosera burmannii and D. indica,
are often collected for their perceived medical benefits (Jayaram
and Prasad, 2006).

3.4. Pollution

Pollution was the third most common 1st level threat to carniv-
orous plants, affecting 18 of the species examined (Fig. 1a). This
category covered different forms of urban waste (solid and
water-borne), fertilizer and pesticide run-off, and various indus-
trial pollutants. Some forms of pollution (such as herbicides)
can be lethal to carnivorous plants directly, while other forms (such
as nutrient addition) have a more indirect effect by degrading
the habitat and making conditions more conducive for other
plants. Two 2nd level category were found to be a threat to carniv-
orous plants, that of agricultural and forestry effluents, and air-
borne pollutants (Fig. 1b). The category of agricultural and forestry
effluents included nutrient loading from fertilizer run-off, herbic-
icide run-off, and soil erosion, and affected 16 of the 18 species.
Air-borne pollutants (in the form of nitrogen deposition), were a
threat to the two other species, Drosera anglica (Huntke, 2007)
and Sarracenia purpurea (Gotelli and Ellison, 2002). Additionally,
eutrophication (typically associated with fertilizer run-off from
agriculture) has been implicated in population declines of species
such as Pinguicula vulgaris (Eysink and De Bruijn, 1997), Utricularia
fibrosa (Morgan and Philipp, 1986), and U. purpurea (Vaithyanathan
and Richardson, 1999).

Fig. 1. Number of species affected by 1st level threat categories (a), and number of species affected by 2nd level threat categories (b). Numbers in parentheses correspond to
the classification proposed by Salafsky et al. (2008).
3.5. Natural systems modifications

The fourth most common threat to carnivorous plants was natural systems modifications, affecting 17 species (Fig. 1a). The 2nd level threats for this category included fire and fire suppression, dams and water management/use, and other modifications of the natural environment intended to improve human quality of life (Fig. 1b). These actions will typically cause carnivorous plant habitat to be degraded, but they can also result in loss of habitat. Indeed, fire suppression and drainage have been implicated as major causes of decline in suitable habitat for many carnivorous plant genera in the southeastern United States, such as Sarracenia (Folkerts, 1982). For example, fire suppression can be harmful to carnivorous plants as it allows other non-carnivorous plants to encroach and out-compete them for light and nutrients. Water management changes are also capable of severely degrading the habitat for carnivorous plants, as even small drainage ditches can reduce the water level enough so that they are unable to survive. Other natural system modifications found to be threats to carnivorous plants included the addition of lime to watersheds (Mackun et al., 1994), reduced grazing (Hugot, 2009), and reduced mowing (Folkerts, 1977).

4. Discussion

The most commonly documented threats to carnivorous plants were habitat loss from agriculture, collection of plants from the wild, and pollution. While habitat loss is known to be a major threat to biodiversity worldwide, over-collection in particular seems to be a much greater threat to carnivorous plants when compared with most other taxa (Gurevitch and Padilla, 2004). The most common threats to carnivorous plants may also differ considerably even from other plants within the same country. For example, in the United States Wilcove et al. (1998) found that habitat loss and degradation, followed by invasive species, were the most common threats to plant species. In comparison, we found pollution, followed by habitat modification and over-collection to be the most common threats to carnivorous plants in the United States. It is also interesting to note that all of the 11 1st level threat categories proposed by Salafsky et al. (2008) affected carnivorous plants, indicating that a wide range of challenges lie ahead for their conservation. Furthermore, multiple threats were also very common for species, which suggests that a holistic approach, targeted at the habitat-level of carnivorous plants, may be required for their successful conservation.

Perhaps unsurprisingly, residential and commercial development, natural systems modifications, invasive and other problematic species and genes, and pollution, were closely associated with one another and often combined to threaten species. Natural system modifications, invasive species, and pollution are all likely to be facilitated by urbanization, yet the documented pollution threats were almost exclusively from agricultural and forestry effluents. Thus, carnivorous plants may be affected by effluents at a considerable distance from the source of the pollution. Agriculture and biological resource use (predominantly collection of plants from the wild) were not closely associated with any other threats. This suggests that the agricultural activities threatening carnivorous plants could be taking place away from urban areas, and additionally indicates that the collection of plants may be more common in undisturbed habitats. Nonetheless, it was surprising to find that agriculture was not more closely associated with natural systems modifications and pollution.

The results from the indicator species analysis suggest that Sarracenia spp. are the best indicators of threats from agriculture, over-collection, invasive species, and pollution, while Drosera spp. may also be particularly sensitive to agriculture. It seems unlikely that these two genera alone would be indicative of these...
threats, as they are morphologically very different. Additionally, while our results indicated that Sarracenia may be more sensitive to threats than other genera, considerably more research has been conducted on this genus and thus it is likely that their threats have been more thoroughly documented. Therefore, until more studies are conducted on a wider range of genera, it will be difficult to determine whether Sarracenia truly is a particularly sensitive genus, or if the results are simply a reflection of a bias in research effort.

Given the available data on carnivorous plant threats, we suggest three areas of further study. First, we recommend more empirical studies quantifying the effects of pollution on carnivorous plants. Pollution is known to be an important threat to many taxa (Wilcove and Master, 2005), yet very little empirical research has been conducted examining its effects on carnivorous plants, even though it was widely documented as a threat. For example, while there has been some research on the effects of an herbicide on aquatic carnivorous plants (Smith and Pullman, 1957), no studies have examined their potential effects on terrestrial carnivorous plants. Furthermore, we are not aware of any studies that have examined the effects of insecticides on carnivorous plants. Empirical studies should elucidate the importance of these types of pollutants in carnivorous plant population declines. Second, we believe that it is worth further exploring the potential role of many carnivorous plants as indicator species for ecosystem health. Our rationale is that many species are fairly conspicuous and thus fairly easy to identify, they are often sensitive to changes in environmental conditions such as water levels, and some research has suggested that carnivorous plants can exhibit negative responses to increased levels of nutrients and pollutants (Ellison and Gotelli, 2002; Moody and Green, 2010; Vaitkytė-Than and Richardson, 1999). Unfortunately, as collection from the wild is a major threat to these plants, their use as indicator species could draw attention to their locations, which could ultimately be counter-productive. Third, we recommend more research to quantify the extinction vulnerability of these taxa. While many carnivorous plant species have been assessed by the IUCN in recent years, the vast majority of species on the Red List are pitcher plants, and there are no representatives from the two most speciose carnivorous plant genera, Utricularia and Drosera. However, quantifying extinction risk for carnivorous plants can be complicated by considerable differences in threat statuses at the country-level scale. For example, using the National Red List database (www.nationalredlist.org), we found that the threat status of Utricularia australis from nine countries ranged from least concern to extinct, and broad ranges in threat statuses were also found for other species, such as D. anglica and Pinguicula alpina.

Whilst we are confident that our data collection methods covered the majority of peer-reviewed literature on carnivorous plant conservation threats, we acknowledge several important caveats. Most importantly, there were undoubtedly biases both in the focal species and geographical regions of research, which means that any results extrapolated to all carnivorous plants should be interpreted with caution. For example, while we found 19 species with documented threats in North America, we found only two species with documented threats in Africa, and only one species with any documented threat in Australia. Considering the high diversity of carnivorous plant species found in parts of Africa and Australia, this is almost certainly an underrepresentation of the true threats encountered by species there. Furthermore, there were no documented threats to the genera Brocchinia, Byblis, Catopsis, Cephalotus, Genlisea, Heliamphora, Roridula, and Triphyophyllum, despite several species from these genera being listed as threatened by the IUCN (IUCN, 2010). The biases in focal species and geographical regions of research, combined with the relatively small sample size of documented threats, means that there are likely to be many threats that have thus far gone un-documented. However, we are hopeful that the present study will stimulate further research into the conservation of these plants.

5. Conclusions

Our results clearly demonstrate a need for more research into the threats facing carnivorous plants. Specific documented threats were found for just 48 species, even fewer than the 56 species listed as threatened by the IUCN (2010). Although many carnivorous plants are likely threatened simply because they are highly endemic (often inhabiting isolated bogs or forests), more quantitative data are needed on potential threats actually affecting the remaining 350 or so species. In particular, efforts should focus on those species from underrepresented genera and regions. We are hopeful that our recommendations may actively assist with carnivorous plant conservation, and the present study should draw attention to the dearth of information available for many of these species. Ensuring the conservation of carnivorous plants will not only help maintain the important ecosystem services they provide, but also could prevent secondary extinctions of other specialist species that rely on them.

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