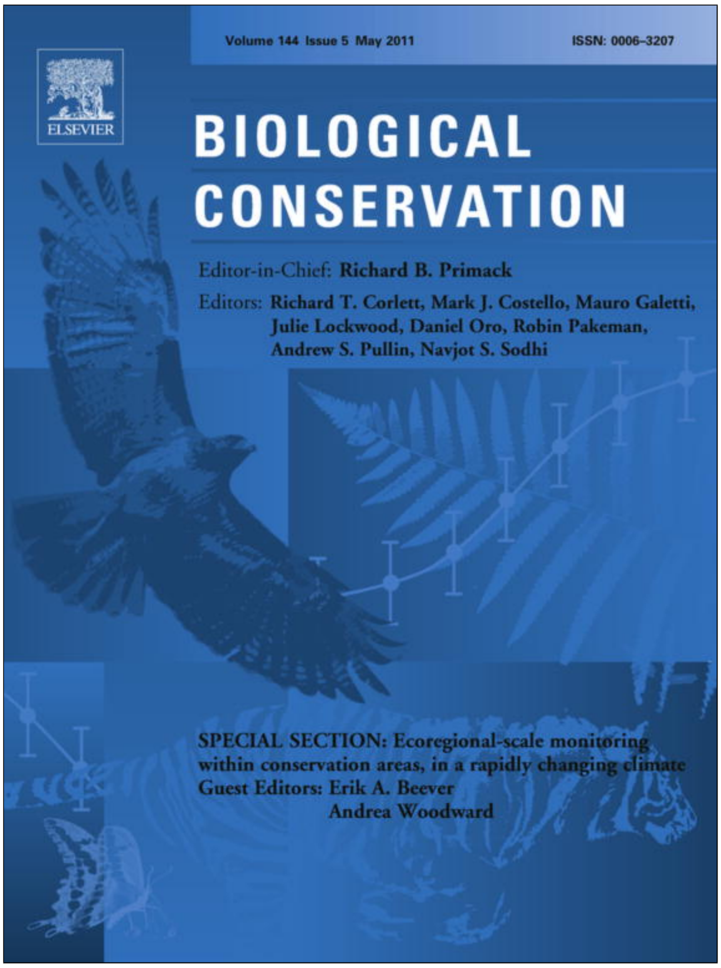
Volume 144 Issue 5 May 2011
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Richard T. Corlett, Mark J. Costello, Mauro Galetti, Julie Lockwood, Daniel Oro, Robin Pakeman, Andrew S. Pullin, Navjot S. Sodhi
SPECIAL SECTION: Ecoregional-scale monitoring within conservation areas, in a rapidly changing climate
Guest Editors: Erik A. Beever
Andrea Woodward

Biological Conservation 144 (2011) 1356–1363

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Review

A review of the conservation threats to carnivorous plants

David E. Jennings *, Jason R. Rohr

Department of Integrative Biology, University of South Florida, 4202 East Fowler Avenue, Tampa, FL 33620, USA

A R T I C L E   I N F O

Article history:
Received 24 October 2010
Received in revised form 3 March 2011
Accepted 14 March 2011
Available online 3 April 2011

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

A B S T R A C T

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.

Contents

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

* Corresponding author. Tel.: +1 813 974 4694.
E-mail address: dejennin@mail.usf.edu (D.E. Jennings).

0006-3207/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2011.03.013

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 digesting 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). Throughout all of these regions, many 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 miricidia 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 Šmilauer, 2002) and the biplot was created using CanoDraw 4.12 to display the ordination results (ter Braak and Šmilauer, 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

Table 1
Carnivorous plant species for which documented threats were found.

Species	1st level threat category[a]											Reference(s)
	1	2	3	4	5	6	7	8	9	10	11	
Aldrovanda vesiculosa	x	x					x		x			Adamec (1995, 2005) and Kundu et al. (1996)
Darlingtonia californica					x							Folkerts (1977)
Dionaea muscipula		x		x	x		x		x			Folkerts (1977) and Luken (2005)
Drosera anglica							x		x			Huntke (2007)
Drosera brevifolia		x										Saridakis et al. (2004)
Drosera burmanii	x	x		x				x	x		x	Jayaram and Prasad (2006)
Drosera cendeensis		x			x							Duno de Stefano and dos Santos Silva (2001)
Drosera communis		x										Saridakis et al. (2004)
Drosera filiformis			x									Freedman et al. (1992) and Landry and Cwynar (2005)
Drosera grievei		x										Lowrie and Marchant (1992)
Drosera indica	x	x		x				x	x		x	Jayaram and Prasad (2006)
Drosera intermedia			x				x					Mackun et al. (1994) and Rassi et al. (2001)
Drosera montana		x										Saridakis et al. (2004)
Drosera sp.		x			x							Duno de Stefano and dos Santos Silva (2001)
Drosera villosa		x										Saridakis et al. (2004)
Drosophyllum lusitanicum	x	x		x								Correia and Freitas (2002) and Garrido et al. (2003)
Nepenthes alata					x							Simpson (1995)
Nepenthes ampullaria					x							Simpson (1995)
Nepenthes bokor	x	x										Cheek and Jebb (2009)
Nepenthes campanulata	x	x										Simpson (1995)
Nepenthes clipeata					x							Simpson (1995)
Nepenthes gracilis					x							Simpson (1995)
Nepenthes gracillima	x				x							Simpson (1995)
Nepenthes khasiana		x	x	x	x		x					Mao and Kharbuli (2002)
Nepenthes northiana			x									Simpson (1995)
Nepenthes rafflesiana					x							Simpson (1995)
Nepenthes thai			x									Cheek and Jebb (2009)
Pinguicula alpina			x				x					Lilleleht (1998)
Pinguicula corsica						x	x	x				Hugot (2009)
Pinguicula fontiqueriana		x			x							Rhazi et al. (2007)
Pinguicula ionantha							x					Folkerts (1977)
Pinguicula reichenbachiana	x			x	x			x				de Belair and Diadema (2008)
Pinguicula vulgaris							x		x			Eysink and De Bruijn (1997)
Sarracenia alabamensis subsp. *alabamensis*					x			x	x			Folkerts (1977)
Sarracenia alabamensis subsp. *wherryi*		x		x								Folkerts (1977)
Sarracenia alata	x	x			x		x	x	x			Schnell et al. (2000a)
Sarracenia flava	x	x			x		x	x	x			Schnell et al. (2000b)
Sarracenia jonesii	x	x			x		x	x	x			Folkerts (1977)
Sarracenia leucophylla	x	x			x		x	x	x			Folkerts (1990) and Schnell et al. (2000c)
Sarracenia minor	x	x			x		x	x	x			Schnell et al. (2000d)
Sarracenia oreophila	x	x			x		x	x	x			Carter et al. (2006), Govus (1987) and Schnell et al. (2000e)
Sarracenia psittacina	x	x			x		x	x	x			Schnell et al. (2000f)
Sarracenia purpurea									x			Gotelli and Ellison (2002)
Utricularia fibrosa									x			Morgan and Philipp (1986)
Utricularia purpurea									x			Vaithiyanathan and Richardson (1999)
Utricularia simulans	x			x			x					Schnell (1980)
Utricularia sp.									x			David (1996)
Utricularia striatula										x		Chaturvedi (2005)

[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.

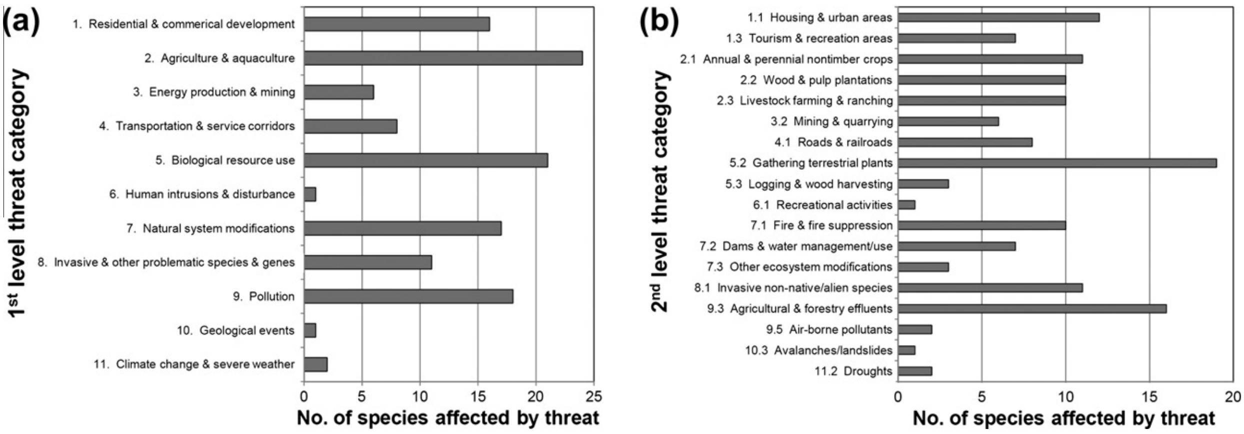

Fig. 1. Number of species affected by 1st level threat categories (a), and number of species affected by 2nd level threat categories (b). Numbers in parentheses correspond to the classification proposed by Salafsky et al. (2008).

modifications (Fig. 1a), and consequently they are the only categories we discuss in detail. Human intrusions and disturbance, and geological events were the two least common 1st level threats with only one affected species each (Fig. 1a). For 2nd level threats, gathering terrestrial plants from the wild was the most common, affecting 19 species, while recreational activities and avalanches/landslides were the least common with only one affected species each (Fig. 1b).

3.1. Principal coordinate analysis

The PCoA revealed that species within a genus often faced similar threats (Fig. 2). For instance, *Sarracenia* species were predominantly affected by natural system modifications, invasive species, pollution, over-collection, and agriculture; *Utricularia* species were predominantly affected by pollution; *Drosera* species were predominantly affected by agricultural activities; and *Nepenthes* species were predominantly affected by over-collection (Fig. 2). The indicator species analyses revealed positive associations among species in the genus *Sarracenia* and agricultural activities (indicator value [IV] = 31.6, $p = 0.045$), over-collection (IV = 32.0, $p = 0.039$), invasive species (IV = 46.8, $p = 0.002$), and pollution (IV = 41.5, $p = 0.011$). We also detected positive associations between *Drosera* species and agricultural activities (IV = 46.0, $p = 0.012$; when excluding *Sarracenia*). Perhaps as a consequence of species within a genus having similar threats, some threats were also positively correlated, with residential and commercial 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 species (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 carnivorous plant species). The threats were fairly evenly distributed among three 2nd level categories. Specifically, annual and perennial 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 also 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 species) (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 persistent 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 burmanii* 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 carnivorous 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 industrial 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 carnivorous 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, herbicide 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* (Vaithiyanathan and Richardson, 1999).

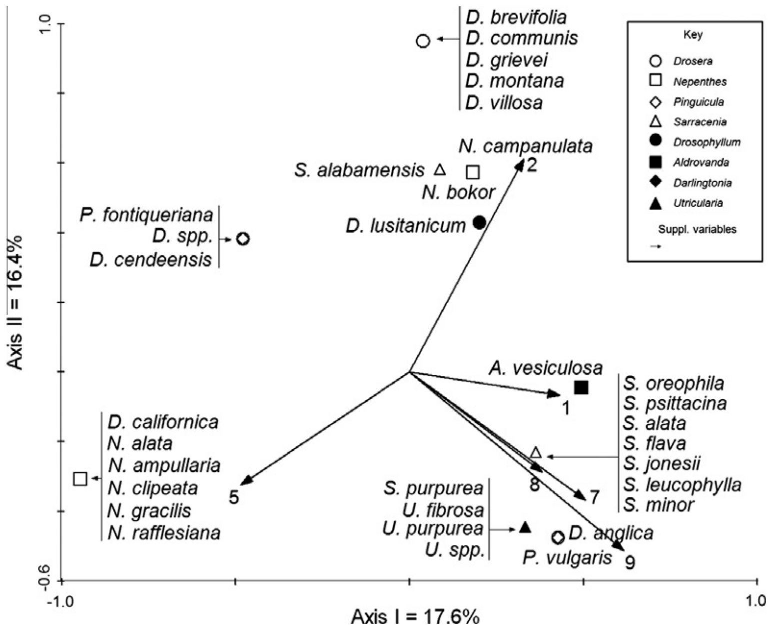

Fig. 2. Results of a principal coordinate analysis (based on Jaccard's distance) of the threats to carnivorous plant species. The 20 principal coordinates used in the analysis have been suppressed and the threat categories have been passively (post-hoc) projected into the ordination space. To reduce clutter in the biplot, we have only displayed species with fits of >20% and threat categories with correlation coefficients outside the range of −0.3 to 0.3. The distance of species and threat categories from the origin indicate their relative importance in the biplot. Perpendicularly projecting the threat categories to the axes provides an estimate of the correlation coefficient of that variable with that axis. The angle between threat categories is negatively proportional to the correlation of those threats. Distance among species approximates the dissimilarity of their threats. Each of the numbered 1st level threat categories shown (arrows in the biplot) correspond to the classification proposed by Salafsky et al. (2008): (1) residential and commercial development, (2) agriculture and aquaculture, (5) biological resource use, (7) natural systems modifications, (8) invasive and other problematic species and genes, and (9) pollution.

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, 1997), 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; Guisande et al., 2000; Moody and Green, 2010; Vaithiyanathan 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 550 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.

Acknowledgements

This work was supported in part by a Fern Garden Club Scholarship, and Rutlish Foundation Grant to D.E.J. We thank members of the Rohr lab, Dr. Richard Primack, and three anonymous reviewers for improving the manuscript.

References

Adamec, L., 1995. Ecological requirements and recent European distribution of the aquatic carnivorous plant *Aldrovanda vesiculosa* – a review. Folia Geobotanica & Phytotaxonomica 30, 53–61.

Adamec, L., 2005. Ten years after the introduction of *Aldrovanda vesiculosa* to the Czech Republic. Acta Botanica Gallica 152, 239–245.

Albert, V.A., Williams, S.E., Chase, M.W., 1992. Carnivorous plants: phylogeny and structural evolution. Science 257, 1491–1495.

Anderson, B., Midgley, J.J., 2002. It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. Oecologia 132, 369–373.

Angerilli, N.P.D., Beirne, B.P., 1974. Influences of some freshwater plants on development and survival of mosquito larvae in British Columbia. Canadian Journal of Zoology-Revue Canadienne De Zoologie 52, 813–815.

Bayer, R.J., Hufford, L., Soltis, D.E., 1996. Phylogenetic relationships in Sarraceniaceae based on rbcL and ITS sequences. Systematic Botany 21, 121–134.

Brewer, J.S., 2001. A demographic analysis of fire-stimulated seedling establishment of *Sarracenia alata* (Sarraceniaceae). American Journal of Botany 88, 1250–1257.

Brewer, J.S., 2003. Why don't carnivorous pitcher plant's compete with non-carnivorous plants for nutrients? Ecology 84, 451–462.

Brinson, M.M., Malvarez, A.I., 2002. Temperate freshwater wetlands: types, status, and threats. Environmental Conservation 29, 115–133.

Buckley, H.L., Miller, T.E., Ellison, A.M., Gotelli, N.J., 2010. Local- to continental-scale variation in the richness and composition of an aquatic food web. Global Ecology and Biogeography 19, 711–723.

Cameron, K.M., Wurdack, K.J., Jobson, R.W., 2002. Molecular evidence for the common origin of snap-traps among carnivorous plants. American Journal of Botany 89, 1503–1509.

Carter, R., Boyer, T., McCoy, H., Londo, A., 2006. Classification of green pitcher plant (*Sarracenia oreophila* (Kearney) Wherry) communities in the Little River Canyon National Preserve, Alabama. Natural Areas Journal 26, 84–93.

Chaturvedi, S., 2005. Conservation strategies of some rare and threatened taxa of Nagaland. National Academy Science Letters-India 28, 345–348.

Cheek, M., Jebb, M., 2009. *Nepenthes* group Montanae (Nepenthaceae) in Indo-China, with *N. thai* and *N. bokor* described as new. Kew Bulletin 64, 319–325.

Clarke, C., Kruger, R., 2006. *Nepenthes tenax* C. Clarke & R. Kruger (Nepenthaceae), a new species from Cape York Peninsula, Queensland. Austrobaileya 7, 319–324.

Clarke, C., Davis, T., Tamin, R., 2003. *Nepenthes izumiae* (Nepenthaceae): a new species from Sumatra. Blumea 48, 179–182.

Clarke, C.M., Bauer, U., Lee, C.C., Tuen, A.A., Rembold, K., Moran, J.A., 2009. Tree shrew lavatories: a novel nitrogen sequestration strategy in a tropical pitcher plant. Biology Letters 5, 632–635.

Correia, E., Freitas, H., 2002. *Drosophyllum lusitanicum*, an endangered West Mediterranean endemic carnivorous plant: threats and its ability to control available resources. Botanical Journal of the Linnean Society 140, 383–390.

Das, I., Haas, A., 2010. New species of *Microhyla* from Sarawak: old World's smallest frogs crawl out of miniature pitcher plants on Borneo (Amphibia: Anura: Microhylidae). Zootaxa 37, 52.

David, P.G., 1996. Changes in plant communities relative to hydrologic conditions in the Florida Everglades. Wetlands 16, 15–23.

de Belair, G., Diadema, K., 2008. *Pinguicula reichenbachiana*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/164088> (downloaded on 05.08.10).

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Duno de Stefano, R., dos Santos Silva, T.R., 2001. Conservation status of the carnivorous genus *Drosera* in South America and the Caribbean. Harvard Papers in Botany 6, 253–260.

Ellison, A.M., Gotelli, N.J., 2002. Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. Proceedings of the National Academy of Sciences of the United States of America 99, 4409–4412.

Ellison, A.M., Gotelli, N.J., 2009. Energetics and the evolution of carnivorous plants – Darwin's 'most wonderful plants in the world'. Journal of Experimental Botany 60, 19–42.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3, 479–486.

Eysink, F., De Bruijn, O., 1997. Restoration of fen meadows in the Lemselermaten. Levende Natuur 98, 258–265.

Feeley, K.J., Terborgh, J.W., 2008. Direct versus indirect effects of habitat reduction on the loss of avian species from tropical forest fragments. Animal Conservation 11, 353–360.

Filippi, E., Luiselli, L., 2000. Status of the Italian snake fauna and assessment of conservation threats. Biological Conservation 93, 219–225.

Folkerts, G.W., 1977. Endangered and threatened carnivorous plants of North America, In Extinction Is Forever. In: Prance, G.T., Elias, T.S. (Eds.), Threatened and Endangered Species of Plants in the Americas and Their Significance in Ecosystems Today and in the Future. Proceedings of a Symposium, Bronx, NY, USA, May 11–13, 1976. New York Botanical Garden, Bronx, New York, USA, pp. 301–313.

Folkerts, G.W., 1982. The Gulf Coast pitcher plant bogs. American Scientist 70, 260–267.

Folkerts, G.W., 1990. The white-topped pitcher plant: a case of precarious abundance. Oryx 24, 201–207.

Freedman, B., Maass, W., Parfenov, P., 1992. The thread-leaved sundew, *Drosera filiformis*, in Nova Scotia – an assessment of risks of a proposal to mine fuel peat from its habitat. Canadian Field-Naturalist 106, 534–542.

Gardner, T.A., Barlow, J., Sodhi, N.S., Peres, C.A., 2010. A multi-region assessment of tropical forest biodiversity in a human-modified world. Biological Conservation 143, 2293–2300.

Garrido, B., Hampe, A., Maranon, T., Arroyo, J., 2003. Regional differences in land use affect population performance of the threatened insectivorous plant *Drosophyllum lusitanicum* (Droseraceae). Diversity and Distributions 9, 335–350.

Gibson, M., Warren, K.S., 1970. Capture of *Schistosoma mansoni* miracidia and cercariae by carnivorous aquatic vascular plants of the genus *Utricularia*. Bulletin of the World Health Organization 42, 833–835.

Gotelli, N.J., Ellison, A.M., 2002. Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*. Ecology 83, 2758–2765.

Govus, T.E., 1987. The occurrence of *Sarracenia oreophila* (Kearney) Wherry in the Blue Ridge province of southwestern North Carolina. Castanea 52, 310–311.

Guisande, C., Andrade, C., Granado-Lorencio, C., Duque, S.R., Nunez-Avellaneda, M., 2000. Effects of zooplankton and conductivity on tropical *Utricularia foliosa* investment in carnivory. Aquatic Ecology 34, 137–142.

Gurevitch, J., Padilla, D.K., 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19, 470–474.

Hayward, M.W., 2009. The need to rationalize and prioritize threatening processes used to determine threat status in the IUCN Red List. Conservation Biology 23, 1568–1576.

Hughey, K.F.D., Cullen, R., Moran, E., 2003. Integrating economics into priority setting and evaluation in conservation management. Conservation Biology 17, 93–103.

Hugot, L., 2009. *Pinguicula corsica*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/157939> (downloaded on 5.08.10).

Huntke, T., 2007. The distribution of *Drosera anglica* Huds. In Lower Saxony past and present – the extent of the decline of a raised bog specialist and its causes. Tuexenia, 241–253.

IUCN, 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org> (downloaded on 05.08.10).

Jayaram, K., Prasad, M.N.V., 2006. *Drosera indica* L. and *D. burmanii* Vahl., medicinally important insectivorous plants in Andhra Pradesh - regional threats and conservation. Current Science 91, 943–946.

Jennings, D.E., Krupa, J.J., Raffel, T.R., Rohr, J.R., 2010. Evidence for competition between carnivorous plants and spiders. Proceedings of the Royal Society B – Biological Sciences 277, 3001–3008.

Juniper, B.E., Robins, R.J., Joel, D.M., 1989. The Carnivorous Plants. Academic Press, London.

Kesler, H.C., Trusty, J.L., Hermann, S.M., Guyer, C., 2008. Demographic responses of *Pinguicula ionantha* to prescribed fire: a regression-design LTRE approach. Oecologia 156, 545–557.

Kundu, S.R., Basu, S., Chakraverty, R.K., 1996. *Aldrovanda vesiculosa* Linn. – its maiden appearance and disappearance from India: a review. Journal of Economic and Taxonomic Botany 20, 719–724.

Landry, M., Cwynar, L.C., 2005. History of the endangered thread-leaved sundew (*Drosera filiformis*) in southern Nova Scotia. Canadian Journal of Botany-Revue Canadienne De Botanique 83, 14–21.

Lilleleht, V., 1998. Red Data Book of Estonia: Threatened Fungi, Plants, and Animals. Estonian Academy of Sciences, Tartu.

Lowrie, A., Marchant, N., 1992. Four new *Drosera* taxa from south western Australia. Nuytsia 8, 323–332.

Luken, J.O., 2005. Characterizing illegal harvest of the Venus' fly trap (*Dionaea muscipula* Ellis) at Lewis Ocean Bay Heritage Preserve, South Carolina, USA. Natural Areas Journal 25, 295–299.

Mackun, I.R., Leopold, D.J., Jraynal, D.J., 1994. Short-term responses of wetland vegetation after liming of an Adirondack watershed. Ecological Applications 4, 535–543.

Mann, P., 2007. *Drosera gibsonii* (Droseraceae), a new pygmy *Drosera* from south-west western Australia. Nuytsia 16, 321–323.

Mao, A.A., Kharbuli, P., 2002. Distribution and status of *Nepenthes khasiana* Hook. f. – a rare endemic pitcher plant of Meghalaya, India. Phytotaxonomy 2, 77–83.

McCune, B., Mefford, M.J., 1999. PC-ORD: Multivariate Analysis of Ecological Data. Version 4. MjM Software Design, Gleneden Beach, OR.

Moody, C., Green, I.D., 2010. Assimilation of Cd and Cu by the carnivorous plant *Sarracenia leucophylla* Raf. fed contaminated prey. Environmental Science & Technology 44, 1610–1616.

Moon, D.C., Rossi, A.M., Depaz, J., McKelvey, L., Elias, S., Wheeler, E., Moon, J., 2010. Ants provide nutritional and defensive benefits to the carnivorous plant *Sarracenia minor*. Oecologia 164, 185–192.

Moore, P.D., 2002. The future of cool temperate bogs. Environmental Conservation 29, 3–20.

Morgan, M.D., Philipp, K.R., 1986. The effect of agricultural and residential development on aquatic macrophytes in the New Jersey pine barrens. Biological Conservation 35, 143–158.

Rassi, P., Alanen, A., Kanerva, T., Mannerkoski, I., 2001. The Red List of Finnish Species. Ministry of the Environment and Finnish Environment Institute, Helsinki.

Rhazi, L., Grillas, P., Rhazi, M., 2007. *Pinguicula fontiqueriana*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/164235> (downloaded on 05.08.10).

Rivadavia, F., Kondo, K., Kato, M., Hasebe, M., 2003. Phylogeny of the sundews, *Drosera* (Droseraceae), based on chloroplast rbcL and nuclear 18S ribosomal DNA sequences. American Journal of Botany 90, 123–130.

Russell, R.W., 2008. Spring peepers and pitcher plants: a case of commensalism? Herpetological Review 39, 154–155.

Rymal, D.E., Folkerts, G.W., 1982. Insects associated with pitcher plants (*Sarracenia*: Sarraceniaceae), and their relationship to pitcher plant conservation: a review. Journal of the Alabama Academy of Science 53, 131–151.

Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H.M., Collen, B., Cox, N., Master, L.L., O'Connor, S., Wilkie, D., 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. Conservation Biology 22, 897–911.

Saridakis, D.P., Torezan, J.M.D., Andrade, G., 2004. Microhabitat preferences of six *Drosera* (Droseraceae) from Tibagi river basin, Parana State, Brazil. Brazilian Archives of Biology and Technology 47, 495–501.

Schnell, D.E., 1980. Notes on *Utricularia simulans* Pilger (Lentibulariaceae) in southern Florida. Castanea 45, 270–276.

Schnell, D.E., 2002. Carnivorous Plants of the United States and Canada, second ed. Timber Press, Portland, OR.

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000a. *Sarracenia alata*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39713> (downloaded on 05.08.10).

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000b. *Sarracenia flava*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39715> (downloaded on 05.08.10).

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000c. *Sarracenia leucophylla*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39716> (downloaded on 05.08.10).

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000d. *Sarracenia minor*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39717> (downloaded on 05.08.10).

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000e. *Sarracenia oreophila*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39718> (downloaded on 05.08.10).

Schnell, D.E., Catling, P., Folkerts, G.W., Frost, C., Gardner, R., 2000f. *Sarracenia psittacina*, in IUCN 2010. IUCN Red List of Threatened Species. Version 2010.2. <http://www.iucnredlist.org/apps/redlist/details/39719> (downloaded on 05.08.10).

Simpson, R.B., 1995. *Nepenthes* and conservation. Curtis's Botanical Magazine 12, 111–119.

Smith, C.S., Pullman, G.D., 1997. Experiences using Sonar ® A.S. aquatic herbicide in Michigan. Lake and Reservoir Management 13, 338–346.

Sodhi, N.S., Posa, M.R.C., Lee, T.M., Bickford, D., Koh, L.P., Brook, B.W., 2010. The state and conservation of Southeast Asian biodiversity. Biodiversity and Conservation 19, 317–328.

Steinmann, P., Keiser, J., Bos, R., Tanner, M., Utzinger, J., 2006. Schistosomiasis and water resources development: systematic review, meta-analysis, and estimates of people at risk. Lancet Infectious Diseases 6, 411–425.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.

ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5), Ithaca, NY.

Vaithiyanathan, P., Richardson, C.J., 1999. Macrophyte species changes in the everglades: examination along a eutrophication gradient. Journal of Environmental Quality 28, 1347–1358.

van Diggelen, R., Middleton, B., Bakker, J., Grootjans, A., Wassen, M., 2006. Fens and floodplains of the temperate zone: present status, threats, conservation and restoration. Applied Vegetation Science 9, 157–162.

Wilcove, D.S., Master, L.L., 2005. How many endangered species are there in the United States? Frontiers in Ecology and the Environment 3, 414–420.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615.

Zamora, R., Gomez, J.M., 1996. Carnivorous plant slug interaction: a trip from herbivory to kleptoparasitism. Journal of Animal Ecology 65, 154–160.