Biological Conservation 203 (2016) 260–267

Contents lists available at ScienceDirect

Biological Conservation

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

A systematic assessment of threats affecting the rare plants of the United States

Haydée Hernández-Yáñez [a,b], Justin T. Kos [a], Matthew D. Bast [a,c], Janeisha L. Griggs [a], Paul A. Hage [a], Alex Killian [a], M. Isabel Loza [a,b], Matthew B. Whitmore [a], Adam B. Smith [a,b,*]

[a] Department of Biology, University of Missouri-St. Louis, 223 Research Building, One University Boulevard, St. Louis, MO 63121-4499, USA
[b] Center for Conservation and Sustainable Development, Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, MO 63110, USA
[c] St. Louis Community College, Meramec, 11333 Big Bend Boulevard, St. Louis, MO 63122-5799, USA

ARTICLE INFO

Article history:
Received 28 April 2016
Received in revised form 19 September 2016
Accepted 4 October 2016
Available online xxxx

Keywords:
Agriculture
Urbanization
Plants
Invasive species
Recreation
Threats

ABSTRACT

Characterizing the distribution of threats facing species is a crucial, first step toward designing effective conservation strategy. The last comprehensive analysis of threats facing rare plants in the United States was conducted nearly 20 years ago. Here we systematically analyze the threats facing 2733 rare and vulnerable plants in the US using textual analysis of the most comprehensive database available. In the continental US plants are most commonly threatened by outdoor recreation (affecting 35% of species), especially from off-road vehicles (19%) and hiking and related activities (13%). The next-most common threats are from livestock (33%), residential development (28%), non-native invasives (27%), and roads (21%). In Hawaii invasives threaten 95% of species followed by increases in fire intensity/frequency (26%) then livestock (19%). Multivariate analyses indicate threats do not form distinct "syndromes" (clusters of threats) but rather a single "mega-syndrome" with high degrees of overlap between most threats. We also compared the prevalence of threats to the distribution of research effort. Nearly 75% of threats are understudied relative to their prevalence, including five of the six most common threats while a few rare threats (missing species like pollinators; pathogens; logging; climate-induced ecosystem movement; and crop-based agriculture) receive most of the attention. In comparison to a benchmark assessment from 1998 (Wilcove et al. *BioScience* 48:607-615) we find little difference in threat prevalence, though temporal trends suggest increasing frequency of nearly all threats. Overall rare plants in the US are affected by a dense network of threats across which research attention is disproportionately directed.

1. Introduction

Five major threats endanger biodiversity: habitat alteration, overharvest, invasive species, pollution, and disease (Millennium Assessment, 2005) with climate change expected to become yet another driver of biodiversity loss (Thomas et al., 2004). Each of these broadly-defined threats can be further divided into specific threats from diverse factors like urbanization, agriculture, native versus non-native invasive species, and so on. Detailed characterization of threats facing species is crucial for effective recovery planning (Lawler et al., 2002; Hayward, 2009), directing conservation strategy (Murray et al., 2014), allocating resources across conservation actions (Wilson et al., 2007), and estimating the political feasibility of abating threats (Prugh et al., 2010). Hence, there is a pressing need to describe the distribution of threats across species as specifically as possible. The last such analysis for plants in the United States was performed nearly 20 years ago (Wilcove et al., 1998).

Threats can act in concert to affect groups of species (Burgman et al., 2007; Budiharta et al., 2011). For example, agriculture, overexploitation, and urbanization each threaten generally distinct groups of carnivorous plants (Jennings and Rohr, 2011). These threat "syndromes" (sensu Burgman et al., 2007) can be related to geographic co-location of species (Jono and Pavoine, 2012), range size (Burgman et al., 2007; González-Suárez et al., 2013), habitat type (Burgman et al., 2007), taxonomy (Budiharta et al., 2011; McCune et al., 2013), or the fact that some kinds of human activities engender multiple threats to species (e.g., road construction can facilitate spread of invasives). Syndromes offer both opportunities and challenges for managers and researchers. On one hand, addressing sets of co-occurring threats increases efficiency and knowledge transfer because they may have a common origin (Burgman et al., 2007). On the other hand, addressing groups of threats can be difficult if they are diverse in nature and require very different strategies to ameliorate (Auerbach et al., 2015; Tulloch et al., 2016).

For science to adequately inform threat abatement, research effort should be apportioned in rough accordance to the actual incidence

---

* Corresponding author at: Center for Conservation and Sustainable Development, Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, MO 63110, USA.
E-mail address: adam.smith@mobot.org (A.B. Smith).

http://dx.doi.org/10.1016/j.biocon.2016.10.009
0006-3207/

and severity of each threat. Nonetheless, it is likely that some threats receive disproportionate research attention. For example, climate change has gained increasing scientific and public attention in part because it is expected to become a major driver of biodiversity change in the coming century (Thomas et al., 2004). However, some conservation practitioners have warned that devoting too much attention to climate misses widespread, contemporary threats that will not only remain important but interact with climate change to further challenge biodiversity (Novacek, 2008; Tingley et al., 2013). Conservation would be better served if research attention matched the relative severity and distribution of threats facing species.

Here we assess the threats facing 2733 rare plant species in the United States using the most comprehensive database of rare species available (NatureServe, 2014). We used a systematic, transparent, replicable textual analysis to extract threat data for each species from the database. Our objectives were 1) to describe the distribution of threats across species; 2) identify syndromes of co-acting threats; and 3) compare the prevalence of threats across species to research effort devoted toward each threat.

2. Methods

2.1. Database and threat taxonomy

In December 2014 we acquired NatureServe data for all plant species in the US that are globally critically imperiled (NatureServe rounded rank G1—see http://www.natureserve.org/conservation-tools/conservation-status-assessment), imperiled (G2), suspected of being extinct (GH), or listed as threatened or endangered under the US Endangered Species Act (ESA). NatureServe employs a standardized method for assessing species' conservation status based on rarity and overall trend and (since 2012) threats (Faber-Langendoen et al., 2012; Master et al., 2012). The database includes information on 2733 species, subspecies, and varieties (hereafter "species") of vascular and non-vascular plants. For most species there are textual descriptions of threatening factors, though this information is spread across several fields and not necessarily standardized. These descriptions are obtained from multiple sources including field observations, experimental work, and the peer-reviewed and gray literature.

We systematically analyzed these descriptions to classify threats to each species. Threats were classified using the 2.0 Beta version of the IUCN threats taxonomy developed by Salafsky et al. (2008; www.cmp-openstandards.org; Table A.1). The taxonomy is composed of three hierarchical levels, the first (L1) being the most general (e.g., "human intrusions and disturbance") and second (L2) more specific (e.g., "recreation") and the third (L3) the most detailed (e.g., "off-road vehicular recreation"). Not all L2 threats have an associated set of L3 threats. We added one more L1 and associated L2 categories for "other" threats, an additional L2 category for "missing species" (pollinators, grazers, symbionts, hosts), and several custom L3 categories based on a preliminary analysis (Table A.1). Since 2012 status updates by NatureServe have included assessment of threats using the IUCN system (Faber-Langendoen et al., 2012; Master et al., 2012). For these species ($n = 963$) we used the threats as they were recorded but in some cases made changes based on the textual description of threats. Prior to analysis we combined L2 or L3 categories affecting <1% of species with categories in the same higher-level category.

2.2. Replicability, transparency, and uncertainty

The textual descriptions of threats are not standardized and are thus open to alternative interpretations (cf. Hayward, 2009). We developed an extensive rubric populated with examples to ensure different assessors consistently identified threats (Appendix B). Following recent, similar assessments (McCune et al., 2013) we scored a threat regardless of whether the written description expressed uncertainty about the threat. For 23% of the species we also employed a cross-checking system in which pairs of assessors independently rated threats for the same species. Partners were rotated between sets of species. When issues arose the matter was resolved between partners or brought to the larger group. Agreement between assessors was very high (mean Cohen's Kappa = 0.98, minimum value across all species = 0.84; Fig. B.1). Initially we classified threats based on the time period in which they were noted to affect species ("past/present/future"), and whether threats were proximate ("direct"—e.g., industrial effluent) or ultimate ("indirect"—a nearby factory producing the effluent), but found few cases where threats did not occur in the present (1.4% "past", 1.8% "future") or were noted as being indirect (<1%), so we analyzed all threats regardless of their time of effect or causal distance. In the end we scored threats as "1" (threatens the species) or "0" (does not threaten).

Frequently threats could only be identified to a higher-level category. In these cases we assigned the threat to an "unspecified" category for that threat type (e.g., "unspecified transportation/utility corridors"). Upon assessing all species, we then assigned counts from these unspecified threats to each "specified" L2 or L3 threat in the same L1 category in proportion to the number of species in the specified threats. For example, among species threatened by the L1 category transportation/utility corridors, there were 465 affected by the L2 category roads/railroads, 98 by ecological management of rights-of-way, and 97 by utility/service lines. There were also 11 species affected by an unspecified threat from transportation or utility corridor. In this case the number affected by roads/railroads was increased by 7.75 species ($= 11 \times (465 / (465 + 98 + 97))$). We used this reapportioning procedure in all analyses using percentages of species affected by a given threat.

The conservation status of species in the database has been updated over time. To determine if the date of assessment influenced the prevalence of threats we divided species into three 6-year groups based on date of assessment: 1996 through 2002, 2003 through 2008, and 2009 through 2014 (the last year any species in the copy of the database we received was evaluated). We used January 1, 1996 as a cutoff date for the first period because the most comparable study to ours (Wilcove et al., 1998) evaluated species that had been assessed up to this date.

We emphasize that our results are limited by our interpretation of the original descriptions of factors threatening species. Some threats are also more evident than others (e.g., off-road vehicles versus climate change), while others may be over-reported (e.g., the presence of an invasive species may be interpreted to be harmful even if it is not). The descriptions also allow neither assessment of geographic extent, severity of threats, nor whether they act in a sporadic or continuous manner. As a result the prevalence of a threat in our analysis does not necessarily connote its overall role in causing a decline in rare plant diversity. Our analysis is also only able to identify threats that affect species in the present or recent past, and cannot for example, indicate effects of initial agricultural expansion that may have caused species in our data set to become rare in the first place. We also note that status updates are implemented on a rolling basis so do not necessarily reflect the most current threats to each species. The median date of last status update for CONTUS species was February of 2006 while the median date for Hawaiian species was May 1997. Hence, we urge care in interpreting results for Hawaiian species. In all these respects our analysis faces the same limitations experienced by similar studies (e.g., Wilcove et al., 1998; Venter et al., 2006; Burgman et al., 2007; Prugh et al., 2010; McCune et al., 2013). We also note that information on bryophytes in the data set is known to be incomplete or has not been reviewed, but given the small number of bryophyte species ($n = 22$) we did not expect them to bias the analysis and so retained them.

2.3. Identifying threat syndromes

We attempted to identify threat syndromes using multivariate and univariate analysis. Analyses were conducted in the R Version 3.3.1 (R Core Team, 2016) using the "vegan" package (Oksanen et al., 2015).

First, we applied non-metric multidimensional scaling on the matrix of pairwise distances between species calculated using one minus the Jaccard index. The algorithm failed to converge regardless of measures we took to induce convergence (increasing dimensions, iterations, and using the "noshare" argument; Borcard et al., 2011; Oksanen et al., 2015). Thus we tested for clusters of threats using the unweighted pair group method with arithmetic means (UPGMA) on the one minus the Jaccard index calculated between threats. Bootstrap analysis was used to determine support for each node (Efron et al., 1996). We also applied a univariate test to measure the pairwise correlation between threats using Yule's ϕ coefficient of association calculated between each pair of threats. Significance was assessed using a χ^2 test (Chedzoy, 2006).

2.4. Comparing research attention to threat prevalence

To determine how well research effort relevant to threats matches the actual prevalence of threats affecting plants we conducted a systematic literature assessment of articles published in five popular conservation journals: *Biological Conservation*, *Biodiversity & Conservation*, *Conservation Biology*, *Conservation Evidence*, and *Diversity & Distributions.* From these journals we randomly selected publications from the 9883 articles published from 2000 to 2014. We then scanned the title and abstract of each selected article, identifying for further analysis those that focused on plants, included plants as one of their focal groups, or were general in taxonomic nature, and excluding articles that focused exclusively on non-plant taxa. This subset of abstracts was then assessed using the same threats taxonomy used to evaluate species.

We calculated the percentage of articles relevant to each threat type as the number of articles pertaining to a threat divided by the number of articles pertaining to any threat. We stopped selecting articles for analysis when the standard error of percentage of articles in each L2 or L3 category was <0.05%, which occurred when 1307 articles were selected for evaluation, of which 375 pertained to at least one threat. To measure the relative balance of research effort, we first calculated the ratio of percentage of articles relevant to a threat to the percentage of species affected by that threat. Values >1 indicate that the threat receives greater attention than its prevalence across species and <1 that less attention is received. We applied the reapportionment procedure described in Section 2.2 Replicability, transparency, and uncertainty to article counts before comparing them to prevalence of threats affecting species.

3. Results

Not all L2 threats had associated L3 threats, so we generally report results for L2 and only use L3 to provide more detail when possible. Unless otherwise stated, we report results for the continental US including Alaska (CONTUS, 80% or 2194 of 2733 species) and Hawaii (20% or 539 species) separately. Seventy six percent of CONTUS species had one or more threats reported while 90% of Hawaiian species had one or more threats. Hereafter we include all species (with and without any threats noted) when reporting percentage of species affected by each threat. On average CONTUS species were affected by 3.15 ± 2.84 (mean ± SE) threats and Hawaiian species 1.97 ± 1.61. The distribution of L2 threats among all species was highly skewed (Fig. C.1), with a mean of 2.92 ± 3.02, a mode of 0 (21% of species), and a maximum of 19.

3.1. Distribution of threats

Outdoor recreation (L2) was the most common threat in CONTUS, affecting 35% of species (Fig. 1a). Most impacts from recreation were from use of off-road vehicles (ORVs; 19% of species), and hiking, bicycling, trail riding, skiing, and recreational climbing (13%; categories are not exclusive as a species could be affected by multiple threats). The next-most common threats were livestock-based agriculture (33%), residential development (28%), invasive species (27%), and construction and maintenance of roads and railroads (21%). All other threats each affected <20% of species.

Across Hawaiian species (Fig. 1b) the most common threat was from invasive species (95%), followed by change in fire regime, which was entirely due to an increase (versus a decrease) in fire intensity/frequency (26%). The third-most common threat was from livestock (19%). All others each affected <10% of species. In contrast to CONTUS species, only 9% of Hawaiian species were threatened by recreation (5% hiking and related activities, 3% ORVs).

When we divided species into three 6-year periods according to the date their status was last assessed, we found there was a trend toward increasing proportion of species affected through time across nearly all threats (Fig. 2), though the trend was not necessarily monotonic. For example, the incidence of recreation in CONTUS increased from 17 to 38 to 48% of species across the first, second, and latest assessment periods, respectively. Other common threats increased accordingly (livestock: 22, 35, 41%), housing and urban development (24, 32, 28%), invasives (15, 32, 34%), and construction and maintenance of roads (10, 24, 28%). Threats affecting Hawaiian species also tended to increase across assessment periods, though not as dependably (invasives: 91, 83, 97%, fire/fire suppression: 28, 17, 21%).

3.2. Threat syndromes

None of the analyses found evidence for threat syndromes, groups of threats acting together (Figs. 3 and D.1). Bootstrap analysis on UPGMA cluster analysis nodes indicated that in only one case for CONTUS and Hawaii each did any node have >95% support (Fig. D.1). For CONTUS the node split three uncommon threats (unspecified forestry/overharvest, unspecified intrusions, and other) from the others. For Hawaii the node split fire regime change from other threats, suggesting a single-threat syndrome related to an increase in fire intensity/frequency.

The univariate analysis revealed a high degree of positive association between threats (Fig. 3). For CONTUS, across 946 possible pairwise comparisons of L2 threats 46.6% of Yule's ϕ coefficients were significantly positive and only 0.6% significantly negative, whereas chance associations should lead to ~5% of coefficients being significant with a roughly even split between positive and negative associations. For Hawaii 22.7% of ϕ values were significantly positive and none negative. Combined, the multivariate and univariate tests suggest that even though threats do not form syndromes there is a high degree of overlap between threats.

3.3. Research attention

We found large disparities between the prevalence of articles relevant to each threat and the prevalence of threats facing species (Fig. 4). >75% of threats (22 of 29) receive less research attention given their prevalence affecting species. Understudied threats include 5 of the 6 most common threats, including roads/railroads (ratio of percentage of relevant articles to percentage of species affected: 0.74), invasive species (0.60), residential development (0.40), livestock (0.38), and recreation (0.15). Only 24% of threats had ratios >1, indicating research attention is disproportionately directed toward these threats, especially missing species (e.g., pollinators, grazers; ratio of 3.45), pathogens/disease (2.55), logging (1.7), climate-induced ecosystem migration (1.32), crop-based agriculture (1.21), and tree-based agriculture and plantations (1.09).

4. Discussion

Our study provides a systematic analysis of the threats affecting the rare plants of the US using the most comprehensive database available. Although only 29% of the plants in the database are currently listed under the ESA, all of them would likely qualify for listing (Wilcove and Master, 2005). The taxa we analyzed comprise about one eighth of all known plants in the US (Wilcove and Master, 2005). Our key findings

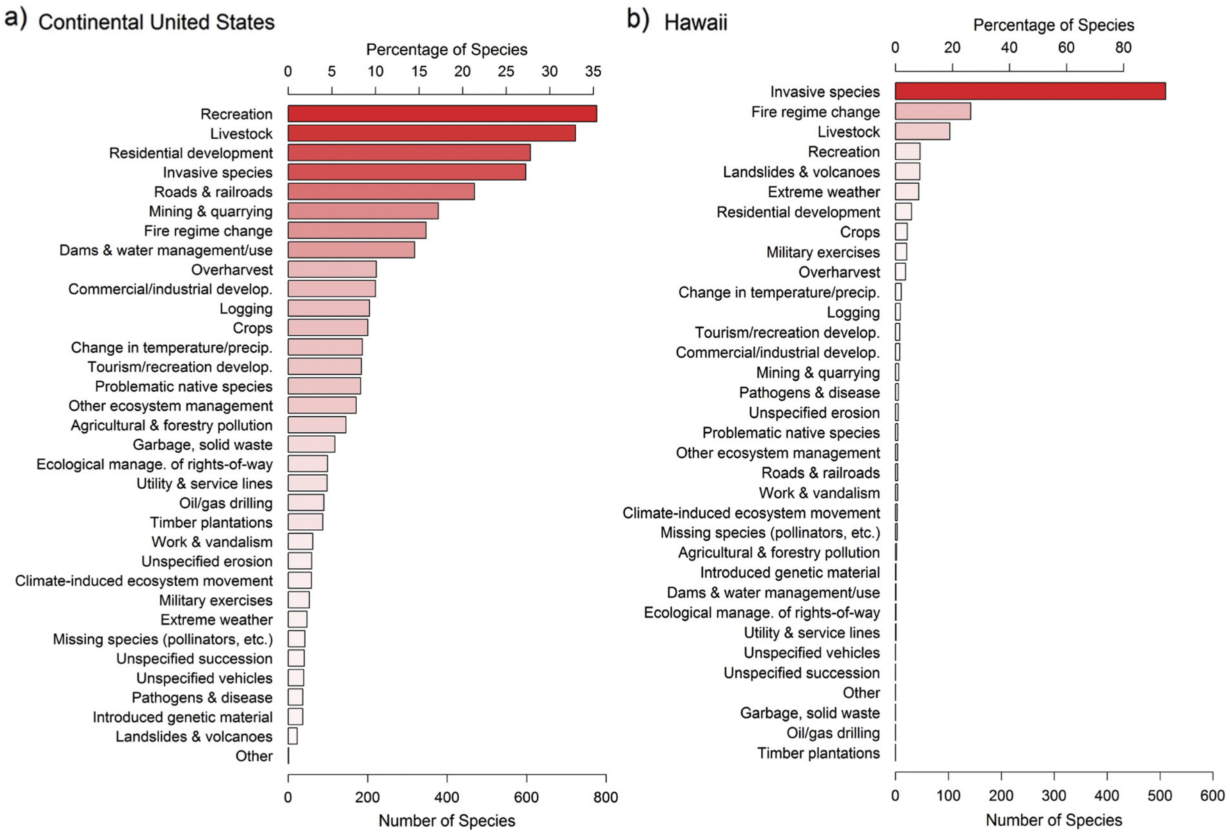

Fig. 1. The distribution of level 2 threats across species (a) in the continental US and (b) in Hawaii. Across the continental US outdoor recreational activities were the most common threat affecting species, followed by livestock, invasives, then roads and railroads. The most common threats affecting Hawaiian species were invasives followed by change in fire regime (comprised entirely of an increase—versus a decrease—in fire frequency/intensity), then livestock. The percentage of species affected by threats sums to >100% because a species can be affected by more than one threat.

are threefold. First, in decreasing order, the most common threats in CONTUS are recreation, livestock, residential development, invasives, and construction and maintenance of roads and railroads (Fig. 1a). Each of these alone affects at least one in five species. In contrast, invasives threaten 95% of Hawaiian species followed by increases in fire frequency/intensity which threatens roughly 1 in 4 (Fig. 1b). We also found evidence suggesting the prevalence of threats is understated or has increased through time (Fig. 2). Second, the high degree of overlap between groups of species affected by different threats forms a single massive syndrome imperiling rare plants in the US (Fig. 3). Finally, research attention is directed toward a few threats that affect a few species, while threats that affect most species are underattended (Fig. 4).

4.1. The distribution of threats across species

Surprisingly, outdoor recreation was the most common threat in CONTUS, affecting 35% of species (Fig. 1a). Threats from recreation were mainly due to ORVs (19% of species), hiking, biking, skiing, trail riding, and recreational climbing (13%), and camping and unspecified recreation (16%). Recreation is also the most common threat facing at-risk Canadian plants (McCune et al., 2013). ORVs, hiking, and related activities can reduce population viability directly from physical damage (Prescott and Stewart, 2014). Recreation can also indirectly threaten populations by encouraging invasive species, compacting soil, reducing soil moisture and organic litter, causing erosion, disrupting pollinators and dispersal, and eutrophication from animal and human waste (Anderson et al., 2015; Pickering et al., 2010). In our analysis indirect effects would have been scored distinctly from recreation. Unfortunately, following the trail of causation from, say, hikers to the spread of invasives is often impossible (Salafsky et al., 2009). Outdoor recreation poses a conundrum for conservation since experiences in nature foster support for conservation (Miller, 2006). Obviously, restricting access to nature at large is not a workable solution. However, targeted re-routing of trails, setting aside land for intensive (e.g., ORV) use, and audience-focused environmental education can help ameliorate these kinds of threats (Graber and Brewer, 1985; Mankin et al., 1999; Borrie and Harding, 2002).

Livestock pose the second-most common threat in CONTUS (33%) and third-most across Hawaiian species (19%; Fig. 1). Livestock can directly harm plants through consumption and trampling (Fleischner, 1994; Belsky et al. 1999) and indirectly through soil compaction, induction of erosion, encouraging invasive species, and alteration of competitive environments, nutrient cycles, and fire regimes (Leip et al., 2015). However, livestock can also increase species diversity and biomass in ecosystems that benefit from herbivore-mediated control of otherwise dominant species. Indeed, some conservation agencies actively use livestock to manage protected areas (Jensen, 2001). However, we found only 39 plants were perceived to be in peril because of “missing” species, and only four of these arose from lack of large ungulates.

Residential development threatens the third-largest set of species (28%) in CONTUS. The direct negative effects of urbanization on biodiversity occur from habitat loss, but also encompass spread of invasives, pollution, habitat alterations, and human intrusions (Grimm et al., 2008), though these would have been scored separately in our analysis.

Invasive species were the most common threat to Hawaiian species, affecting 95% of species (Fig. 1b), and fourth-most common in CONTUS, affecting 26% of species (Fig. 1a). Invasives have diverse effects on native biodiversity that occur directly or indirectly through competition, consumption, and alteration of the physical environment (Strayer et al., 2006; Vila et al., 2011). Despite their ignominy, there remains debate about the effect of invasives on plant communities (Gurevitch and Padilla, 2004a, 2004b; Riccardi, 2004; Vila et al., 2011), with some finding that invasives plants (vs. animals) generally augment local diversity (Sax et al., 2002).

Roads and railroads threatened 21% of plants in CONTUS, 17% of which was due to road construction and maintenance. The prevalence of this threat type might be overstated since roadside habitat is more easily surveyed. However, roadsides can provide critical habitat, especially in areas with wholesale land conversion (Forman and Alexander, 1998; Hopwood, 2008). Direct effects from road construction include habitat alteration, residue from surface coatings, vehicular soil compaction, and dust and winter salt runoff, while they also serve as sources of invasives, pollution, and eutrophication (Forman and Alexander, 1998). We note that 4% of species are threatened by ecological maintenance of rights-of-way such as roadside mowing, herbicide application, scraping, and related activities. Although these activities affect just a small number of species, this type of threat is comparatively easy to address by, for example, shifting timing of mowing (Baskin and Baskin, 2000).

Change in fire regime threatened the second-largest number of Hawaiian species (26%) all of which were affected by an increase in fire frequency/intensity. In contrast, slightly more species on CONTUS were threatened by fire suppression (9%) than an increase in fire (4%—though another 3% could not assigned to either L3 class).

4.2. Temporal trends and comparison with Wilcove et al. (1998)

The most comparable study to ours was conducted nearly 20 years ago by Wilcove et al. (1998). We were unable to replicate their methods exactly, in part because they did not have access to the threats taxonomy by Salafsky et al. (2008). In addition, Wilcove et al. (1998) only counted threats if there was no stated ambiguity about their effect, whereas we followed more recent studies (McCune et al., 2013) and scored threats regardless of whether there was uncertainty expressed in the textual descriptions. However, comparison between the two studies is informative as an indication of temporal changes in the prevalence of threats and as a check on the subjective nature of assessing threats.

Wilcove et al. (1998) examined the distribution of threats relevant to habitat alteration using data for species listed or proposed for listing under the ESA by January 1, 1996. If we restrict our analysis to the same set of species, we find similar percentages of species affected by each threat across the two studies. The few exceptions may be due to methodological differences or actual changes in the prevalence of threats affecting these species since listing (Table 1). We did not observe systematic increases in the proportion of species affected by each threat as would be expected arising from the more conservative scoring system they used. Comparing their analysis of ESA-listed species to all species in our analysis, we also find broad similarities (Table 1). The one notable exception is species affected by crop-based agriculture, which

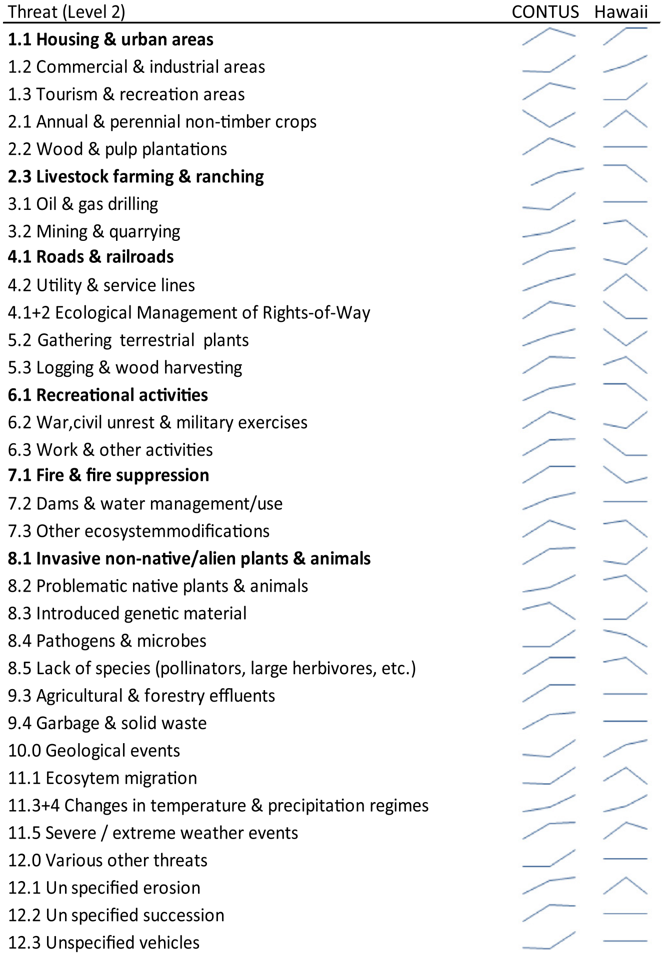

Fig. 2. Temporal trends in percentage of species affected by each threat in the continental US and Hawaii. Species were divided into three 6-yr periods spanning 1996 to 2014 according to the year their status was last updated. Sparklines for each threat show the trend in proportion of species affected by the threat across the three periods. For each sparkline the percentage affected in the first period is on the left and last period on the right. Sparklines are scaled by the overall prevalence of each threat (e.g., a large change in a sparkline for one threat is not necessarily commensurate with a large change in a sparkline for another threat). Nearly all threats increased in prevalence across time in CONTUS and many increased in Hawaii. The six most common threats to plants in CONTUS (across all assessment periods) and single most common threat in Hawaii are in bold.

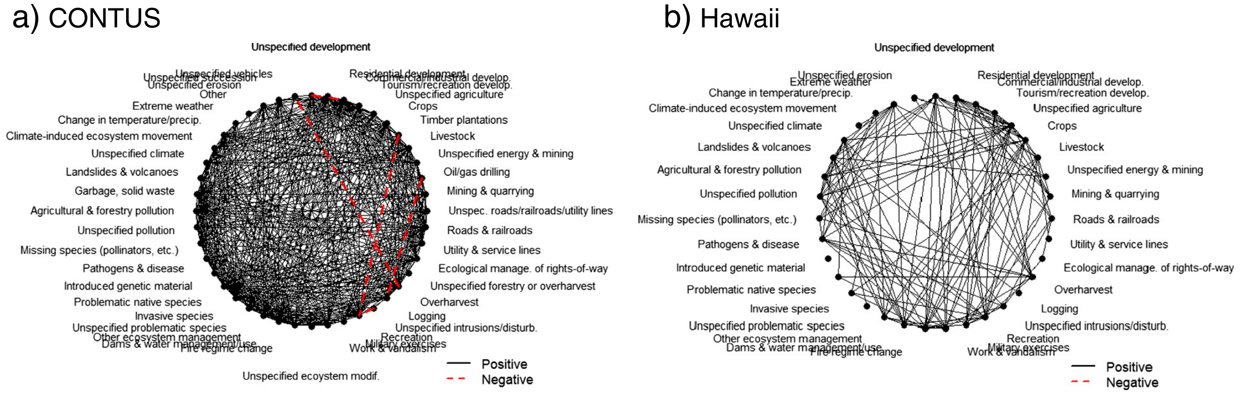

Fig. 3. Pairwise associations between threats in (a) the continental US and (b) Hawaii. Threats are arranged on a circle. Lines connect threats if their pairwise ϕ coefficient was significantly positive or negative. In both cases the large majority of significant associations were positive, indicating threats in the continental US and Hawaii form “mega-syndromes”. Only threats affecting >0 species are shown.

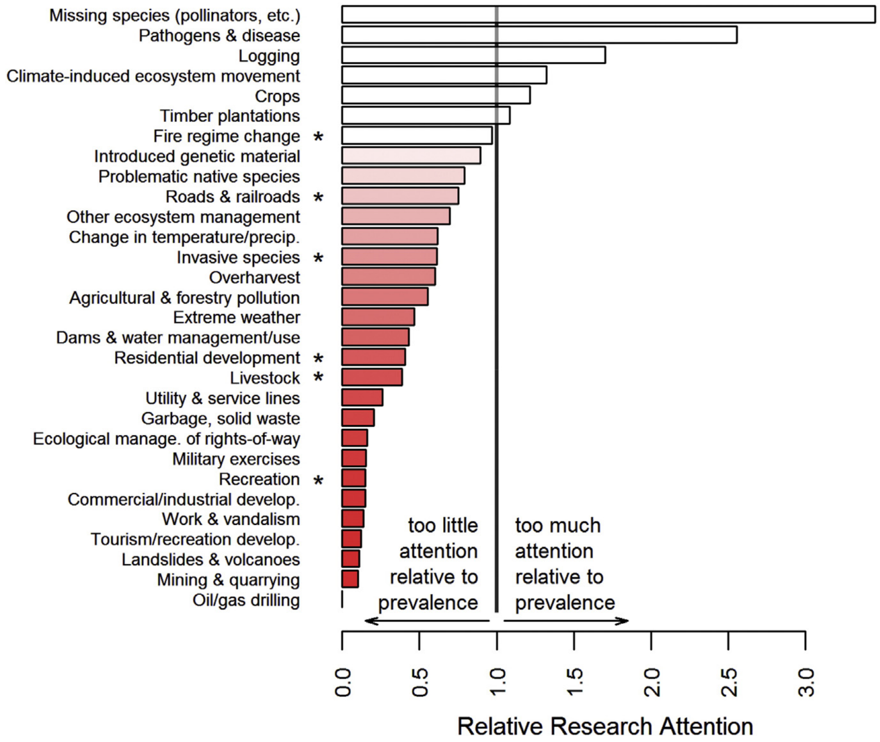

Fig. 4. Research attention devoted to individual threats relative to their prevalence affecting species. Bars indicate the ratio of percentage of articles pertaining to a threat to the percentage of species affected by a threat. Values > 1 indicate research attention is overly focused on that threat and < 1 that research attention is misdirected relative to the prevalence of that threat. The six most common threats facing all species are noted with an asterisk. Only one of them (change in fire regime) receives attention roughly in proportion to its prevalence affecting species; the remainder is relatively understudied.

threatened 33% of ESA-listed species in their study but just 9% of the larger set of species in our analysis. This discrepancy is likely due to the additional species in our dataset, not just methodological differences, since the percentage of ESA-listed species in our dataset affected by crop-based agriculture (31%) was similar to the percentage of species affected in theirs (33%). Hence, the percentage of species actually threatened by crop-based agriculture may actually be fairly low. Comparison of our results to a second analysis in Wilcove et al. (1998) also finds similar prevalence of more broadly-defined threats (Table E.2).

Table 1
Comparison of this study with Wilcove et al. (1998) who analyzed species listed or proposed for listing under the US Endangered Species Act using detailed threat categories specific to habitat degradation/loss. Threat categories are from Box 1 and Table 2 in Wilcove et al. (1998) and were matched as closely as possible to threat categories used in this study. Column values represent percentage of species affected by the given threat. Values in the columns "Wilcove et al." and "ESA" pertain to species listed under the ESA or proposed for listing by January 1, 1996 (the same set analyzed by David Wilcove and colleagues).

		This study	
Threat	Wilcove et al.	ESA	All
Urban & commercial development[a]	36	44	31
Crop-based agriculture	33	31	9
Livestock-based agriculture	33	32	27
Recreation (including ORVs)	33	38	29
Recreation: ORVs	16	23	15
Infrastructure (including road construction & maintenance)[b]	20	23	20
Infrastructure: road construction & maintenance	17	18	16
Disruption of fire regime	20	34	18
Water development (including dams)	15	18	11
Water development: dams	5	2	1
Mining, oil, gas, & geothermal exploitation[c]	11	20	16
Logging & logging roads[d]	7	9	8
Pollution	7	15	9
Military activities	5	3	3

[a] Our values include development related to recreation; this is also included in Wilcove et al. (1998).

[b] Our values include ecological management of utility lines and service corridors; also be included in Wilcove et al. (1998).

[c] Wilcove et al. (1998) include roads constructed for supporting these activities.

[d] Wilcove et al. (1998) include logging roads and associated impacts.

We found increasing levels of threat across time when dividing species by the date their status was last updated (Fig. 2). The percentage of species affected by each threat increased for almost all threats in CONTUS and many threats in Hawaii. One explanation for the rising trend in threat prevalence is that species assessed earlier do indeed have lower rates of threat, though we cannot suggest plausible reasons for why this would be. Alternatively, if they do reflect temporal trends then this suggests that the actual incidence of threats has increased through time. On the other hand, if the differences are due to changes in assessment methodology (Faber-Langendoen et al., 2012; Master et al., 2012), then the actual incidence of threats may be higher than we report since species that were assessed at earlier dates have fewer threats assigned to them than species assessed at later dates.

4.3. Threat syndromes and mega-syndromes

We found little evidence for threat syndromes (Figs. 3 and D.1). Lack of syndromes could occur if threats affect species independently of one another. In this case significant associations between threats should be uncommon and distributed evenly among positive and negative associations. However, threats were overwhelmingly positively associated despite the lack of groups (Fig. 3). In essence, we found threats facing rare plants in the US form a single "mega-syndrome" in which there is a large degree of overlap between threats, a situation also faced by mammals worldwide (Jono and Pavoine, 2012). In light of the diversity of threats affecting species, some have called for a hybrid "coarse- and fine-scale" conservation strategy in which whole communities are targeted for protection while singular populations of rare species are guarded in smaller preserves (Wilcove and Master, 2005; Lindenmayer et al., 2007). Our analysis was conducted at a coarse scale (i.e., counting threats affecting any populations of a species, versus accounting for threats affecting individual populations), so it is more relevant to conservation measures with regional or national perspectives. At the opposite end of the spectrum, fine-scale approaches like preservation of small, select areas harboring rare populations can also be challenged by multiple threats acting in concert (Parker, 2012). We agree the best way forward is combining coarse- and fine-scale approaches but nevertheless contend that the co-occurrence of threats is challenging.

Our results contrast with other assessments that did find groupings of threats which are related to taxonomy, geography, range size, or habitat (Burgman et al., 2007; Budiharta et al., 2011; Jono and Pavoine, 2012; González-Suárez et al., 2013; McCune et al., 2013). Initially we intended to test whether syndromes we identified were related to these factors, but given the lack of groupings among threats, the analysis would have been superfluous. The differences between our results and others do not seem to arise from number of species (Jono and Pavoine, 2012 analyzed all mammals) or taxonomic differences (Burgman et al., 2007 and Budiharta et al., 2011 analyzed plants). Perhaps the long history of intensive development, invasion, cultivation, and land use in the US has created a situation in which multiple human activities compound one another to threaten species.

4.4. The distribution of threats and research attention

Our analysis focuses exclusively on plants in the US; plants elsewhere face a different distribution of threats (Burgman et al., 2007; Budiharta et al., 2011). Hence, using our species assessment as a benchmark against which to measure research effort risks leaving the impression that research should be tailored to address problems facing plants in the US. This is not the message we wish to impart. Moreover, our analysis does not indicate that research on any particular threat is adequate per se—indeed, even "over-studied" threats deserve more research. Likewise, we did not analyze the numerous sources of information in the non-peer reviewed literature or assess threat severity, geographic scope or temporal consistency. Nonetheless, comparing the distribution of threats discussed in the conservation literature to the distribution of threats facing US species does inform us of how well conservation of this particular suite of species is served by the peer-reviewed scientific literature. On this basis we found a gross mismatch between research focus and threat prevalence (Fig. 4). About 75% of threats were understudied relative to their prevalence. A handful received attention roughly appropriate or more than appropriate to their prevalence. Especially troubling are common threats from recreation, livestock, and residential development, all of which affect a large number of species yet receive comparatively little research attention (Fig. 4). While the major obstacles to effective plant conservation are lack of funding, legal protection, and enforcement (Negrón-Ortiz, 2014; Evans et al., 2016), the resources that are available could be directed more efficiently were research attention better tailored to the severity and distribution of threats across species.

5. Conclusions

In descending order, the most common threats to plants in the continental US include outdoor recreation (especially from ORVs and hiking and related activities), livestock, invasives, then construction and maintenance of roads and railroads plus their berms. Alarmingly, there is some evidence that these threats are either understated or increasing in prevalence. None of these threats receive attention in the peer-reviewed scientific literature that is proportionate to their actual prevalence in the United States.

Our results paint a formidable conceptual and strategic challenge for conservation. Rare plants in the US face a complex "mega-syndrome" in which threats act coincidentally to affect non-exclusive groups of species. Thus there seems to be no simple, highly-effective strategy that can alleviate threats to the majority of species at once. Rather, integrated coarse-scale strategies like setting aside land for preservation combined with fine-scale strategies like spot control of invasives or educating and diverting recreationists within established parks will be necessary to address the diversity of threats facing plants in the United States. We do note that inspiring work is developing methods for addressing multiple threats at regional scales (e.g., Conlisk et al., 2013; Auerbach et al., 2015; Tulloch et al., 2016), but more work needs to be done to extend these techniques across scales. We hypothesize that mega-syndromes arise as a product of diverse patterns of land use and exploitation associated with complex economies. If this is indeed the case, then novel conceptual tools and plans of action are required to address the mega-syndrome of threats facing rare plants.

Acknowledgements

We thank Matthew A. Albrecht, J. Leighton Reid, Amanda D. Williams, two reviewers at NatureServe, and two anonymous reviewers for helpful comments on the analysis and manuscript. Lynn Kutner facilitated access to the NatureServe database. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.10.009.

References

Anderson, L.G., Rocliffe, S., Haddaway, N.R., Dunn, A.M., 2015. The role of tourism and recreation in the spread of non-native species: a systematic review and meta-analysis. Public Libr. Sci. ONE 10, e0140833.

Auerbach, N.A., Wilson, K.A., Tulloch, A.I.T., Rhodes, J.R., Hanson, J.O., Possingham, H.P., 2015. Effects of threat management interactions on conservation priorities. Conserv. Biol. 29, 1626–1635.

Baskin, C.C., Baskin, J.M., 2000. Seed germination ecology of *Lesquerella lyrata rollins* (Brassicaceae), a federally threatened winter annual. Nat. Areas J. 20, 159–165.

Belsky, A.J., Matzke, A., Uselman, S., 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. J. Soil Water Conserv. 54, 419–431.

Borcard, D., François, G., Legendre, P., 2011. Numerical Ecology with R. Springer, New York.

Borrie, W.T., Harding, J.A., 2002. Effective recreation visitor communication strategies: Rock climbers in the Bitterroot Valley, Montana. USDA Forest Service Research Note RMRS-RN-15.

Budiharta, S., Widyatmoko, D., Irawati, Rugayah, H.W., Partomihardjo, T., Ismail, Uji, T., Keim, A.P., Wilson, K.A., 2011. The processes that threaten Indonesian plants. Oryx 45, 172–179.

Burgman, M.A., Keith, D., Hopper, S.D., Widyatmoko, D., Drill, C., 2007. Threat syndromes and conservation of the Australian flora. Biol. Conserv. 134, 73–82.

Chedzoy, O.B., 2006. Phi-coefficient. Encyclopedia of Statistical Sciences. John Wiley and Sons, Inc., Hoboken, NJ.

Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A., Regan, H., 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. Glob. Chang. Biol. 19, 858–869.

Efron, B., Halloran, E., Holmes, S., 1996. Bootstrap confidence levels for phylogenetic trees. Proc. Natl. Acad. Sci. U. S. A. 93, 13429–13434.

Evans, D.M., Che-Castaldo, J.P., Crouse, D., Davis, F.W., Epanchin-Neil, R., et al., 2016. Species recovery in the United States: Increasing effectiveness of the Endangered Species Act. Issues in Ecology No. 20. Ecological Society of America, Washington, DC.

Faber-Langendoen, D., Nichols, J., Master, L., Snow, K., Tomaino, A., Bittman, R., Hammerson, G., Heidel, B., Ramsay, L., Teucher, A., Young, B., 2012. NatureServe Conservation Status Assessments: Methodology for Assigning Ranks. NatureServe, Arlington, VA.

Fleischner, T.L., 1994. Ecological costs of livestock grazing in western North America. Conserv. Biol. 8, 629–644.

Forman, R.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.

González-Suárez, M., Gómez, A., Revilla, E., 2013. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. Ecosphere 4, 1–16.

Graber, R.E., Brewer, L.G., 1985. Changes in the population of the rare and endangered plant *Potentilla robbinsiana* Oakes during the period 1973 to 1983. Rhodora 87, 449–457.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global change and the ecology of cities. Science 319, 756–760.

Gurevitch, J., Padilla, D.K., 2004a. Are invasive species a major cause of extinctions? Trends Ecol. Evol. 19, 470–474.

Gurevitch, J., Padilla, D.K., 2004b. Response to Riccardi. Assessing species invasions as a cause of extinction. Trends Ecol. Evol. 19, 620.

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

Hopwood, J.L., 2008. The contribution of roadside grassland restorations to native bee conservation. Biol. Conserv. 141, 2632–2640.

Jennings, D.E., Rohr, J.R., 2011. A review of conservation threats to carnivorous plants. Biol. Conserv. 144, 1356–1363.

Jensen, M.N., 2001. Can cows and conservation mix? Conservationists, ranchers, and scientists attempt to preserve biodiversity and the cowboy way of life. Bioscience 51, 85–90.

Jono, C.M.A., Pavoine, S., 2012. Threat diversity will erode mammalian phylogenetic diversity in the near future. Public Libr. Sci. ONE 7, e46235.

Lawler, J.J., Campbell, S.P., Guerry, A.D., Kolozsvary, M.B., O'Connor, R.J., Seward, L.C.N., 2002. The scope and treatment of threats in endangered species recovery plans. Ecol. Appl. 12, 663–667.

Leip, A., Billen, G., Garnier, J., Grizzetti, B., Lassaletta, L., Reis, S., Simpson, D., Sutton, M.A., de Vries, W., Weiss, F., Westhoek, H., 2015. Impacts of European livestock production: nitrogen, sulphur, phosphorus and greenhouse gas emissions, land-use, water eutrophication and biodiversity. Environ. Res. Lett. 10, 115004.

Lindenmayer, D.B., Fischer, J., Felton, A., Montague-Drake, R., D. Manning, A., Simberloff, D., Youngentob, K., Saunders, D., Wilson, D., M. Felton, A., Blackmore, C., Lowe, A., Bond, S., Munro, N., P. Elliott, C., 2007. The complementarity of single-species and ecosystem-oriented research in conservation research. Oikos 116, 1220–1226.

Mankin, P.C., Warner, R.E., Anderson, W.L., 1999. Wildlife and the Illinois public: a benchmark study of attitudes and perceptions. Wildl. Soc. Bull. 27, 465–472.

Master, L., Faber-Langendoen, D., Bittman, R., Hammerson, G.A., Heidel, B., Ramsay, L., Snow, K., Teucher, A., Tomaino, A., 2012. NatureServe Conservation Status Assessments: Factors for Evaluating Species and Ecosystem Risk. NatureServe, Arlington, VA.

McCune, J.L., Harrower, W.L., Avery-Gomm, S., Brogan, J.M., Csergo, A.-M., Davidson, L.N.K., Garani, A., Halpin, L.R., Lipsen, L.P.L., Lee, C., Nelson, J.C., Prugh, L.R., Stinson, C.M., Whitney, C.K., Whitton, J., 2013. Threats to Canadian species at risk: an analysis of finalized recovery strategies. Biol. Conserv. 166, 254–265.

Millennium Assessment, 2005. Ecosystems and Human Well-being: Current State and Trends. Volume 1. Island Press, Washington.

Miller, J.R., 2006. Restoration, reconciliation, and reconnecting with nature nearby. Biol. Conserv. 127, 356–361.

Murray, K.A., Verde, L.D., Arregoitia, V., Davidson, A., Di Marco, M., Do Fonzo, M.M.D., 2014. Threat to the point: improving the value of comparative extinction risk for conservation analysis. Glob. Chang. Biol. 20, 483–494.

NatureServe, 2014. NatureServe Explorer: An Online Encyclopedia of Life. http://explorer.natureserve.org/; (accessed 2014-12-10).

Negrón-Ortiz, V., 2014. Pattern of expenditures for plant conservation under the Endangered Species Act. Biol. Conserv. 171, 36–43.

Novacek, M.J., 2008. Engaging the public in biodiversity issues. Proc. Natl. Acad. Sci. U. S. A. 105 ((Supplement 1), 11571–11578.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. Package "vegan.". https://cran.r-project.org/web/packages/vegan (accessed 2015-12-12).

Parker, S., 2012. Small reserves can successfully preserve rare plants despite management challenges. Nat. Areas J. 32, 403–411.

Pickering, C.M., Hill, W., Newsome, D., Leung, Y.F., 2010. Comparing hiking, mountain biking and horse riding impacts on vegetation and soils in Australia and the United States of America. J. Environ. Manag. 91, 551–562.

Prescott, O.L., Stewart, G.B., 2014. Assessing the impact of human trampling on vegetation: a systematic review and meta-analysis of experimental evidence. PeerJ 2, e360.

Prugh, L.R., Sinclair, A.R.E., Hodges, K.E., Jacob, A.L., Wilcove, D.S., 2010. Reducing threats to species: threat reversibility and links to industry. Conserv. Lett. 3, 267–276.

R Core Team, 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria URL https://www.R-project.org/.

Riccardi, A., 2004. Assessing species invasions as a cause of extinction. Trends Ecol. Evol. 19, 619.

Salafsky, N., Butchart, S.H.M., Salzer, D., Stattersfield, A.J., Neugarten, R., Hilton-Taylor, C., Collen, B., Master, L.L., O'Connor, S., Wilkie, D., 2009. Pragmatism and practice in classifying threats: reply to Balmford et al. Conserv. Biol. 23, 488–493.

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. Conserv. Biol. 22, 897–911.

Sax, D.F., Gaines, S.D., Brown, J.H., 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. Am. Nat. 160, 766–783.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L., 2006. Understanding the long-term effects of species invasions. Trends Ecol. Evol. 21, 645–651.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148.

Tingley, M.W., Estes, L.D., Wilcove, D.S., 2013. Climate change must not blow conservation off course. Nature 500, 271–272.

Tulloch, A.I.T., Mortelliti, A., Kay, G., Florance, D., Lindenmayer, D., 2016. Using empirical models of species colonization under multiple threatening processes to identify complementary threat mitigation strategies. Conserv. Biol. 30, 867–882.

Venter, O., Brodeur, N.N., Nemiroff, L., Belland, B., Dolinsek, I.J., Grant, J.W.A., 2006. Threats to endangered species in Canada. Bioscience 56, 903–910.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, J., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.

Wilcove, D.S., Master, L.L., 2005. How many endangered species are there in the United States? Front. Ecol. Environ. 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.

Wilson, K.A., Underwood, E.C., Morrison, S.A., Klausmeyer, K.R., Murdoch, W.M., Reyers, B., Wardell-Johnson, G., Marquet, P.A., Rundel, P.W., McBride, M.F., Pressey, R.L., Bode, M., Hoekstra, J.M., Andelman, S., Looker, M., Rondinini, C., Kareiva, P., Shaw, M.R., Possingham, H.P., 2007. Conserving biodiversity efficiently: what to do, where, and when. Public Libr. Sci. Biol. 5, 1850–1861.