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ELTON REVIEW 4

When does invasive species removal lead to ecological recovery? Implications for management success

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Abstract The primary goal of invasive species management is to eliminate or reduce populations of invasive species. Although management efforts are often motivated by broader goals such as to reduce the negative impacts of invasive species on ecosystems and society, there has been little assessment of the consistency between population-based (e.g., removing invaders) and broader goals (e.g., recovery of ecological systems) for invasive species management. To address this, we conducted a comprehensive review of studies (N = 151) that removed invasive species and assessed ecological recovery over time. We found positive or mixed outcomes in most cases, but 31% of the time ecological recovery did not occur or there were negative ecological outcomes, such as increases in non-target invasive species. Ecological recovery was more likely in areas with relatively little anthropogenic disturbance and few other invaders, and for the recovery of animal populations and communities compared to plant communities and ecosystem processes. Elements of management protocols, such as whether invaders were eradicated (completely removed) versus aggressively suppressed (≥90% removed), did not affect the likelihood of ecological recovery. Our findings highlight the importance of considering broader goals and unintended outcomes when designing and implementing invasive species management programs.

Keywords Invasive species · Ecological recovery · Management success · Eradication · Removal

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Introduction

Today, few regions of the world are free of non-native species with most areas being home to multiple, interacting non-native species (van Kleunen et al. 2015). Globally, non-native species are second to land use change in their disruptive impacts on ecological systems (Wilcove et al. 1998; Sala et al. 2000). Invasive species impact ecological systems by disrupting species interactions (Prior and Hellmann 2010; Prior et al. 2015a), causing declines in populations of endangered or endemic species (Courchamp et al.

2003; Vredenburg 2004), altering native biodiversity (Alvarez and Cushman 2002; Clavero and Garcia-Berthou 2005; Powell et al. 2011), influencing ecosystem processes (Vitousek and Walker 1989; Lovett et al. 2006), and shifting ecosystems to alternative states (Brooks et al. 2004; Croll et al. 2005). A major incentive for managing invasive species is to alleviate or reverse their impacts on ecological systems. Developing economical and effective solutions to achieve this goal is a major challenge for scientists, managers, and policy makers (Lodge et al. 2006).

It is generally accepted that the most economical and effective ways to manage invasive species is to prevent their introduction or to detect them early and try to eradicate them before they cause noticeable impacts (Leung et al. 2002; Lodge et al. 2006). However, for already established and damaging species, it is too late to employ such preventative approaches, and managers need to make decisions about how to manage established invasive species and invaded ecosystems. Managers can choose to implement control or eradication programs, or to not employ management (Myers et al. 2000; Hulme 2006). Control programs aim to reduce populations of target invaders to a level in which their impacts are likely to be reduced. Eradication programs aim to eliminate or extirpate populations from a given area (Myers et al. 1998, 2000). When feasible, eradication is a more ideal approach because, in theory, it is a one-time and permanent solution that is most likely to completely alleviate impacts of invasive species on ecosystems and society (Wittenberg and Cock 2001; Brokerhoff et al. 2010; McGeoch et al. 2010). While achieving eradication is feasible in some instances, it is challenging for many cases including for species that are difficult to detect, that occur in habitats where reinvasion is likely, and that have established over large areas (Myers et al. 1998, 2000; Simberloff 2001; Clout and Veitch 2002; Kiett et al. 2011; Pluess et al. 2012; Tobin et al. 2014).

Removing invasive species is the primary goal of invasive species management efforts (Zavaleta et al. 2001; Hulme 2006; Hobbs and Richardson 2011). Success is assessed when the invader is eliminated or suppressed; yet determining these outcomes can be logistically difficult (Myers et al. 2000; Regan et al. 2006; Morrison et al. 2007; Rout et al. 2014). Invasive species management is also motivated by broader goals, such as to alleviate the impacts of invasive species on ecosystems and society (Myers et al. 1998, 2000). The United States Executive Order 13112 on Invasive species (1999) guidelines instruct that federal and state agencies should, "prevent the introduction of invasive species and to provide for their control to minimize the economic, ecological, and human health impacts that invasive species can cause." Thus, population-level management should be viewed as a proximate goal towards broader or ultimate goals of alleviating the impacts of invasive species on ecosystems and society (Zavaleta et al. 2001; Hulme 2006; Regan et al. 2006; Hobbs and Richardson 2011; Suding 2011). Despite these broader goals, the actions of most invasive species management efforts focus on population management of the invader, and the outcome of management is often not evaluated beyond if the invader has been successfully eradicated or suppressed (Myers et al. 1998, 2000; Zavaleta et al. 2001; Reid et al. 2009; Hobbs and Richardson 2011; Kettenring and Adams 2011; Schweizer et al. 2016).

In natural ecosystems, invasive species management is motivated by conservation goals, such as to alleviate invader impacts and to facilitate the recovery of populations of endangered or endemic species, native biodiversity, species interactions, or ecosystem processes or services (Zavaleta et al. 2001; D'Antonio and Meyerson 2002; Nogales et al. 2004; Campbell and Donlan 2005; Bellingham et al. 2010). However, invasive species management may not always alleviate impacts or promote ecological recovery. For example, the management activity itself can have direct negative impacts, such as the effects of aerial spraying of pesticides, poison baits, or the release of biological control agents on non-target species (Courchamp et al. 2003; Louda et al. 2003). Invasive species removal can also have indirect negative effects on ecological systems by altering ecological interactions in ways that simply removing invaders will not alleviate their impacts or allow for recovery (Zavaleta et al. 2001). For example, removing an invader may not alleviate impacts or may even have detrimental effects if they leave behind a legacy effect with long lasting impacts on ecosystems (Corbin and D'Antonio 2012), if they have replaced a functionally important native species (Zarnetske et al. 2010; Buckley and Han 2014), or if their removal causes the release of other more damaging invasive species ("surprise or secondary effects") (sensu Zavaleta et al. 2001; e.g., Courchamp et al. 2003; Bergstrom et al. 2009; Plentovich et al. 2009). Monitoring and determining the outcome of invasive species management programs is largely not evaluated in broad ecological context (Zavaleta et al. 2001; Denslow and D'Antonio 2005; Reid et al. 2009; Kettenring and Adams 2011; Abella 2014; Schweizer et al. 2016).

Removing invasive species and allowing for passive recovery of ecological systems operates under the assumption that ecological communities are resilient to invaders, such that removal will allow systems to recover to pre-invaded states (Jager and Kowarik 2010). In some cases, this is true, and removal leads to ecological success (Jones et al. 2016). The removal of feral goats from Santa Cruz Island, California allowed for the ecosystem to shift back to its pre-invaded woodland ecosystem from a grassland ecosystem (Beltran et al. 2014). Ceasing stocking and removing trout from mountain streams allowed for the increase of the endangered Mountain yellow-legged frog, *Rana muscosa* (Vredenburg 2004). Perhaps most successful have been the eradication of vertebrate predators from islands in allowing for the conservation gains of populations of native animals (Jones et al. 2016). Thus, invasive species removal should remain a necessary step in the recovery of invaded or degraded ecosystems. However, there are also numerous examples in which ecological systems do not recover or recover along an alternative trajectory when invasive species are removed (Zavaleta et al. 2001; e.g., Bullock et al. 2002; Plentovich et al. 2009; Magnoli et al. 2013). If the goal of the invasive species management program is to alleviate the impacts of invasive species on ecological systems, then focusing solely on managing invader populations can lead to undesirable ecological consequences or the misallocation of scarce funds and efforts, which can erode perceived effectiveness of and public support for invasive species management more broadly (Myers et al. 2000; Zavaleta et al. 2001). Thus, invasive species population management should more cautiously be viewed as one component of a more holistic management program that aims to manage whole invaded ecosystems (Atkinson 2001; Zavaleta et al. 2001; Zavaleta 2002; Hulme 2006).

To assess the relationship between success according to invasive species population control (i.e., removal) and broader goals, we conducted a comprehensive, systematic review of the potential for ecological recovery after invasive species removal. We conducted a systematic review by searching for published studies that have successfully eradicated or aggressively suppressed invasive species and measured if removal resulted in positive, neutral, or negative outcomes for ecological systems. We ask several questions. First, how often does population-level management of the invader lead to the broader goal of alleviating ecological impacts of the invader? Second, in what circumstances or contexts is the potential for ecological recovery most likely? In particular, do characteristics of the invader or the invaded ecosystem determine the potential for ecological recovery? Do certain elements of management activates increase the potential for recovery (i.e., eradication vs. suppression)? Our goal is to leverage information from published studies to provide insight into optimal management strategies for invaded ecosystems. We synthesize our results with results from other reviews that have evaluated eradication success (Rejmánek and Pitcairn 2002; Kiett et al. 2011; Pluess et al. 2012; Tobin et al. 2014) to provide guidance into when post-removal management activities will likely be necessary to achieve both proximate (invader removal) and ultimate (ecological recovery) management goals.

Assessing ecological recovery after invasive species management has been discussed in the literature with several review papers on this topic. The most comprehensive review is the seminal review by Zavaleta et al. (2001), who advocated for a whole ecosystem approach to invasive species management. Our study provides an update to this review, by evaluating an additional 135 studies published since 2002, and by employing a systematic and quantitative approach (Fig. 1a). Some quantitative reviews have been conducted on this topic, focusing on particular groups of invaders, such as for the removal and response of invasive plants (Reid et al. 2009; Kettenring and Adams 2011), the removal of invasive goats and rabbits from islands (Schweizer et al. 2016), and of invasive predators from islands (Lavers et al. 2010; Buxton et al. 2014; Jones et al. 2016). However, as far as we are aware, our dataset on this topic is the most comprehensive to-date. Reviewing management efforts quantitatively is an important step to reveal generalizations and improve our ability to predict and provide information to managers for when unwanted

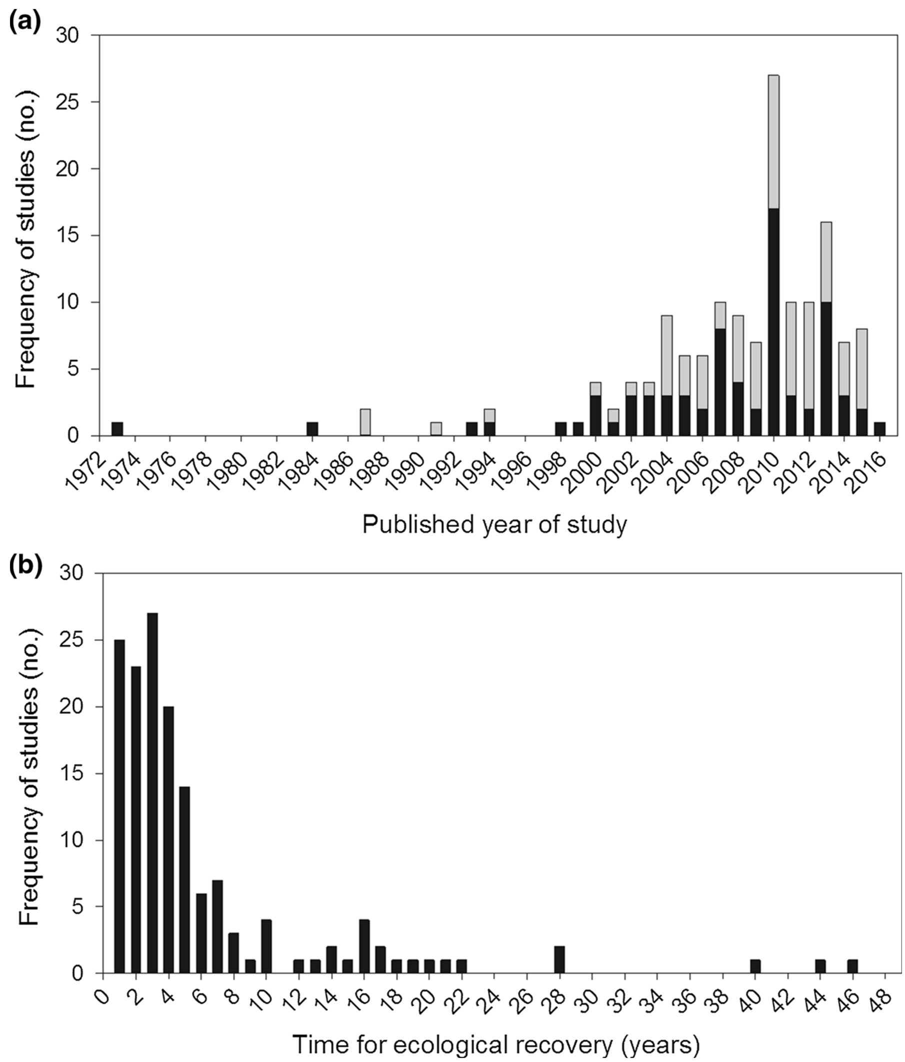


Fig. 1 **a** The frequency of studies that have been published over time (years). *Black bars* represent the number of studies that were scored as positive ecological recovery, and *grey bars* as all other outcomes. **b** The frequency of the number of studies that assessed ecological recovery for different lengths of time post removal (years) (N = 151 studies)

consequences of population-level management may occur.

Materials and methods

Search methods and selection criteria

We conducted a broad search for studies in the peer-reviewed literature that removed invasive species and assessed ecological recovery over time. First, we searched for studies that cited and were cited in several major review papers on invasive species management (Zavaleta et al. 2001; Kettenring and Adams 2011; Pluess et al. 2012; Tobin et al. 2014; Jones et al. 2016). We also searched for papers that were cited and cited reviews on invasive species impacts (Vila et al. 2011; van Hengstum et al. 2014; Gallardo et al. 2015; Cameron et al. 2016). We conducted forward and backward searches of all of the studies that we included in our review. Finally, we conducted targeted keyword searches to explore underrepresented groups (aquatic species, and terrestrial insects). We searched the Web of Science using the keyword search (inv* OR exotic OR "non native" OR introduced AND eradication OR removal OR suppression AND recovery OR response OR impact AND insect OR arthropod OR invertebrate OR aquatic). Our search recovered

Table 1 List of invasive species that were removed in the 151 studies

Taxonomic/functional group	Invader species
Primary producers	
Aquatic plants and algae	*Spartina angilica* (6), *Phragmites australis* (5), *Myriophyllum spicatum* (2), *Ranuculus* spp. (1)
Grasses	*Microstegium vimineum* (2), *Ammophila breviligulata* (1), *Arundo donax* (1), *Cenchrus echinauts* (1), *Eragrostis lehmanniana* (1), *Imperata cylindrical* (1), *Megathyrsus* (1), *Pennisetum setaceum* (1), *Schedonorus phoenix* (1), *Schizachyrium condensatum* (1)
Forbs	*Alliaria petiolata* (2), *Carpobrotus edulis* (2), *Gypsophila paniculata* (2), *Coronilla varia* (1), *Foeniculum vulgare* (1), *Hesperis matronalis* (1)
Shrubs	*Tamarix ramosissima* (7), *Lonicera maackii* (3), *Elaeagnus angustifolia* (2), *Cytisus scoparius* (1), *Frangula alnus* (1), *Lantana amara* (1), *Ligustrum sinense* (1), *Lupinus arboreus* (1), *Rhamnus frangula* (1)
Trees	*Acacia longifolia* (3), *Eucalyptus camaldlunsis* (3), *Acacia mearnsii* (2) *Macaranga mappa* (1), *Melastoma* (1), *Pinus halepensis* (1), *Pittosporum undulatum* (1), *Psidium cattleianum* (1), *Rhizophora mangle* (1), *Solanum mauritianum* (1)
Invertebrates	
Aquatic	*Centrostephanus rodgersii* (1), *Orconectes virilis* (1)
Phytophagous insects	*Aegilops triuncialis* (1)
Ants, wasps	*Pheidole megacephala* (5), *Solenopsis invicta* (2), *Vespula pensylvanica* (1)
Vertebrates	
Small herbivore or omnivores	*Oryctolagus cuniculus* (5), *Trichosurus vulpecula* (1)
Pig	*Sus scrofa* (11)
Ungulates	*Capra hircus* (10), *Cervus elaphus* (4), *Odocoileus virginianus* (2), *Ovis aries* (2), *Bos*. sp. (1), *Rangifer tarandus* (1)
Rodents	*Rattus exulans*, *R. norvegicus*, *R. rattus* (20); *Mus musculus* (5)
Carnivores	*Felis cattus* (7), *Mustela ermine* (1), *Herpestes auropunctatus* (1)
Fishes	*Salvelinus fontinalis* (9), *Oncorhynchus mykiss* (6), *Micropterus dolemieu* (2), *Micropterus salmoides* (2), *Alosa pseudoharengus* (1), *Gila bicolor* (1), *Pseudorasbora parva* (1)

The number of studies pertaining to each species is in parenthesis. In some studies, multiple invasive species were removed

151 studies over 68 genera (Fig. 1a; Table 1; see Electronic supplementary material A). Searching ended in May 2016.

We applied three selection criteria for studies to be considered in our review. (1) The study needed to confirm that the invasive species was removed from the ecosystem. Thus, we focused on studies that either successfully eradicated invasive species or aggressively suppressed species for the duration of monitoring. We defined aggressive suppression as a 90% decrease in the population of the invader (between the control and treatment, see below). Control methods included chemical control, mechanical control, manual removal (hand weeding or trapping), or fencing. We did not include studies that controlled invasive species via biological control, as this is often a less aggressive management activity, and we wanted to focus on the potential for ecological recovery when the invader was mostly removed. We also wanted to focus on studies that targeted removal of the focal invader(s), leaving other species largely intact. For this reason, we did not include management practices with broad impacts such as burning or grazing. (2) The study needed to measure ecological recovery at a minimum of one-year post management. We chose one year as the cutoff to increase the number of studies in our review in underrepresented groups, and we include recovery time as a predictor variable in our models (see "Statistical analysis" section). Ecological assessment post invasive species management ranged from 1 to 46 years, with a mean of 6.1 years (Fig. 1b). We did not include studies that employed active management activities, such as repopulating native species, given that we were interested in the potential for ecological recovery when invasive species reduction was the only management activity.

(3) Ecological recovery was assessed as a change in several types of conservation targets: a population change of a native species, a community level change (e.g., biomass of a group species or diversity), or a change in an ecosystem process (e.g., erosion control, nutrient levels). There were two main types of study designs. Trajectory designs monitored ecological recovery as changes in ecological systems pre and post invasive species removal. Snapshot designs monitored ecological recovery in plots or sites with and without invasive species. We included studies that were a part of management efforts, but we also leveraged information from invader removal experiments designed to test the effect of a management treatment or the impact of invasive species as these experiments can be informative in understanding ecological responses to removal. If studies were conducted as part of the same experiment or management activity and measured the recovery of the same conservation target, we only included the most recent study. Studies were included if they had an appropriate "treatment" (invader removal) and "control" (invader present).

Defining the success of management or restoration activities is challenging. In general, outcomes are often defined as having quick and complete recovery, partial success with some degree of improvement, little or no recovery, or negative outcomes (Zavaleta et al. 2001; Suding 2011). We scored ecological recovery at the study level if the outcomes fell into one of these categories as determined by the results of the studies and conclusion of the authors. A study had a "positive outcome" when invader removal allowed for or was moving towards positive ecological recovery, such as when there was an increase in the population of a native species or native species richness, or if an ecosystem process moved towards a beneficial or pre-invaded state. A study was scored as having a "negative outcome" when there was a decrease in native species or native species richness, or a negative change in an ecosystem response, or an increase in more damaging invasive species or invasive species richness. "No change" occurred, when there were no changes in species or ecosystem processes. Finally, an outcome was scored as a "mixed outcome" in cases in which some elements recovered. For example, there was an increase in the populations of some native species but not others, or in the richness of exotic (i.e., non-damaging) species, or a positive change in one conservation target but not others in which the authors did not rank one being a more desirable conservation outcome than another (e.g., increased native species richness, but a negative change in an ecosystem process).

We collected additional information from the studies, or other sources when necessary for several other factors that could influence the potential for ecological recovery. These included factors that directly relate to our a priori research questions of how characteristics of the invader or invaded ecosystem, or elements of management influence the potential for ecological recovery. We also collected information on other factors that may influence the potential for recovery such as genera, the conservation target, and the biogeographical region (see Table 2 for a full list of factors).

Statistical analysis

We calculated the proportion of studies under each ecological outcome. This vote counting approach can suffer from the "file-drawer problem," in that there could be a bias towards studies that report positive outcomes because studies with outcomes of no or negative effects are likely to be under-published (Rosenthal 1979). We argue that our dataset is largely immune to this issue because the outcome of removing an invasive species on ecological systems is an interesting, publishable result if it is positive, neutral or negative (Suding 2011; Crouzeilles et al. 2016). Our evidence for a lack of publication bias in our dataset also includes that almost half (49%) of cases did not report positive outcomes, and that ratio of positive to not positive outcomes is consistent over time (Fig. 1a).

We scored studies that we categorized as positive ecological recovery as a "1" and all other outcomes as "0." Several other quantitative reviews have scored the outcome of management programs in this binary way (i.e., successful or not) and have conducted model comparisons to explore factors that facilitate success or recovery (see below) (e.g., Pluess et al. 2012; Tobin et al. 2014). Scoring recovery as positive or not allowed us to compare recovery among different scenarios which was necessary given the broad scope of our review.

Table 2 List of factors used as predictor variables, and description of levels with each factor

Factor	Description
Characteristics of invader and invaded ecosystem (fixed effects)	
Taxonomic and trophic group of the invader	Primary producer, invertebrate, vertebrate herbivore, vertebrate predator
Ecosystem	Aquatic, terrestrial mainland, terrestrial island
Anthropogenic disturbance level	Low: restricted access or low recreational use park AND no other reported invaders; moderate: recreational park, rural settlement OR "low" with reported invaders; high: urban area, agriculture area, harvested forest, urban park, dammed waterway, and reported invaders OR "moderate" with reported invaders
Length of invasion time	Length of time in (years) from introduction to removal
Elements of management activities (fixed effects)	
Management area	Size (ha) of management or experimental area (log-transformed)
Time for recovery	Length of time (year) of ecological surveys post removal (log-transformed)
Population-level outcome	Eradicated: completely removed from area; suppressed: partially removed from area
Insularity of management area	Isolated: removed from whole island or water body (pond or lake); continuous: removed from subset of an island, continent or water body (part of a river)
Single or multiple invaders removed	Single removal, multiple removal
Additional factors (random effects)	
Genera of invader	Genera name
Conservation target	Plant community, animal population, animal community, ecosystem process
Biogeographic region	Nearctic, Palearctic, Afrotropical, Indomalayia, Australasia, Neotropic, Oceania, Antarctic
Reason for removal	Managed, experiment

We specified generalized linear models (GLM) with binomial error distributions for a subset of the predictor variables (Table 2) and selected the best-fit models by comparing Akaike information criterion (AIC) scores. We included predictor variables that addressed each of our research questions. First, we ran models with predictor variables pertaining to the characteristics of the invader or invaded ecosystem: the taxonomic and trophic group of the invader, the ecosystem, the length of the time the invader has been established (years; log-transformed) based on information collected from the study or other references, and if the habitat is anthropogenically disturbed, based on its land-use and if it has multiple invaders (see Table 2). Second, we ran models with predictor variables pertaining to the effects of elements of management programs: management area (ha; log-transformed), the length of time in which ecological recovery was assessed (years; log-transformed); if the population was eradicated or suppressed; if the management area was more isolated (e.g., island, lake or pond) or more continuous, and if single or multiple invaders were removed (see Table 2 for definitions of categories). We treated all variables as fixed effects in models. None of our fixed factor variables were correlated in the full dataset (Spearman's $R < 0.70$).

We also expected that several other factors could influence the potential for ecological recovery, including the conservation target, the taxonomic identity (genera) of the invader, or the biogeographical region (Table 2). We tested these as random effects in the models by running generalized linear mixed models (GLMM). First, we examined which random factor(s) to include in the models by comparing AIC scores for models with each of the fixed factor predictor variables with no random effect to models with each random factor. We chose to use the random structure for the models with the lowest AIC scores. Models including conservation target as a random factor had the lowest AIC scores compared to the intercept only and the other random factor models (AIC scores: intercept only = 208.4, conservation target = 202.5, genera = 210.5, biogeographical region = 210.5).

We calculated AIC scores for all of the invader/invaded ecosystem predictor variables separately, and in all combinations (4 factors in total, 16 models, Electronic supplementary material B). We also calculated AIC scores for each of the management factors separately (of which there were 5). We removed the factor with the highest AIC score (multiple invaders; Electronic supplementary material B) as to not overcomplicate the suite of models and to be able to compare this set of models with the first set (we ended up with four factors in total, 16 models). We removed two studies that had missing data for some of the factors to make the models comparable. We then compared all the models, along with an intercept model (random effect only). Changes in AIC scores were calculated along with AIC weights (Electronic supplementary material B). We selected the parsimonious models with the most likely predictor variables by selecting models with a change in AIC ≤ 2 (Burnham and Anderson 2002). Models were also selected only if the AIC value of a complex model was less than the AIC value of the simpler model to avoid selecting overly complex models (Richards 2008).

We conducted similar analyses for each conservation target separately (animal population, animal community, plant population, ecosystem process). Within these smaller datasets, some predictor variables were correlated (Spearman's $R^2 > 0.70$), and models with at least two correlated variables were not included in the list of models to be compared. Given that there were fewer observations and thus power for models for ecosystem responses, we chose to only include three factors each (with the lowest AIC scores) of the management and ecological factors (Electronic supplementary material B). For these within conservation target analyses, we calculated and compared AICc scores to correct for the use of smaller sample sizes. For each model that we retained after selection, we report the P values from the GLM, and report the results of Tukey's posthoc tests in cases in which there are multiple levels of variables (Table 3).

All analyses were performed in R version 3.1.3 (2015). We used the function *glmer* in the package lme4 for the Generalized linear mixed models (Bates et al. 2015), and the AICcmodavg package with several functions to calculate and compare AIC and AICc scores (Mazerolle 2016).

Results

We found 151 studies that documented ecological responses to invasive species removal that satisfied our selection criteria (see Electronic supplementary material A). Of these, most were in terrestrial systems, in which 59 removed vertebrate invaders, 48 plant invaders, and 9 invertebrate invaders (7 of these were ants). In aquatic systems, plant invaders were removed in 20 studies, vertebrate invaders in 17 (all fish), and invertebrate invaders in 2 (Table 1). The number of studies of removals on islands and mainland continents were approximately equal, 72 and 79 respectively. The majority of studies were motivated by management (92), with 52 being experimental tests of impacts, with no difference in the potential for ecological recovery between these two types of removals (GLM: $P = 0.817$).

Positive outcomes of invader removal occurred in 51% of the studies, and 18% of studies reported mixed outcomes. No recovery or no change occurred in 11% of cases and negative outcomes including increases in other invaders or undesirable changes in ecosystem processes (e.g., decreased nutrient retention, increased erosion) occurred in 20% of the cases (Fig. 2).

Out of all of the models in the full dataset, the model with anthropogenic disturbance as the predictor variable had the lowest AIC score (Table 3). Disturbance had a significant effect on the potential for ecological recovery ($\chi^2_{2,145} = 35.52$, $P = 0.031$), with recovery being highest in minimally disturbed sites (with no other documented invaders) and lowest in highly disturbed sites with multiple invaders (Fig. 3a). After model selection, the intercept model was the only other model retained in the set of parsimonious models (Table 3, Electronic supplementary material B). Animal populations responded positively in 76% of the cases followed by animal communities (55%), with plant communities and ecosystem responses only recovering in 33 and 44% of cases respectively ($\chi^2_{4,144} = 186.99$, $P = 0.001$; Fig. 3b).

No factor pertaining to management was retained after model selection (Electronic supplementary material B). For example, there was an equal chance of ecological recovery post management if a species was successfully eradicated (49%) compared to if a species was suppressed (51%) ($P = 0.925$; Fig. 4a).

Table 3 AIC scores, weights, and K of models retained after model selection along with significance of factors (GLM or GLMM)

Factor	AIC/AICc	ΔAIC/AICc	K	AIC/AICc weight	Significance
Full dataset					
Disturbance	200.76	0	3	0.19	*
Intercept	202.51	1.76	2	0.08	–
Animal population					
Disturbance	48.58	0	2	0.2	n.s.
Intercept	49.16	0.58	1	0.15	–
Animal community					
Insularity	61.16	0	2	0.16	*
Taxonomic group	61.76	0.6	3	0.11	*
Plant community					
Taxonomic group + disturbance	90.73	0	3	0.19	Disturbance = *
					Taxonomic = n.s.
Disturbance + ecosystem	92.68	1.95	4	0.44	Disturbance = n.s
					Ecosystem = n.s
Ecosystem processes					
Population management	23.99	0	2	0.19	**
Area	25.13	1.15	2	0.11	*
Recovery time	25.46	1.48	2	0.09	*

The full AIC tables in Electronic Supplementary Material B

AIC values were calculated for the full dataset, and AICc values for the conservation unit datasets. Final models were selected if the change in AIC was less than 2 and if it is not more complicated than the best-fit model. Significance for each variable in the final models was assessed by conducting binomial GLM or GLMM (* $P < 0.05$; ** $P < 0.01$). We did not run GLM on the intercept only model (–)

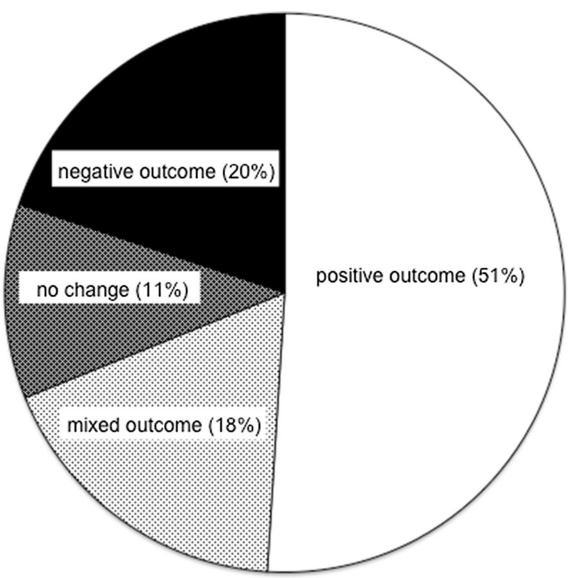


Fig. 2 The percentage of studies that were scored as a positive outcome, mixed outcome, no change, or negative outcome (N = 151 studies)

In the within conservation target group comparisons recovery was influenced by different predictor variables. For animal population recovery, disturbance and the intercept model (in this case with no predictor variable) were retained, but the effect of disturbance was not significant ($\chi^2_{2,37} = 4.29$, $P = 0.257$; Table 3). Animal communities had a higher potential for ecological recovery in continuous compared to isolated management areas ($\chi^2_{2,43} = 56.87$, $P = 0.036$; Table 3), and when invertebrate invaders were removed compared to vertebrate or plant invaders ($\chi^2_{2,42} = 55.18$, $P = 0.047$). In the plant community recovery comparison, two models were retained each with two predictor variables (Table 3). Disturbance was the only significant variable in both of these models ($\chi^2_{2,63} = 82.93$, $P = 0.022$). Finally, there were several models retained in the ecosystem level comparison (Table 3). Ecological recovery at the ecosystem level was higher when invasive species were eradicated versus suppressed ($\chi^2_{2,16} = 19.24$, $P = 0.008$),

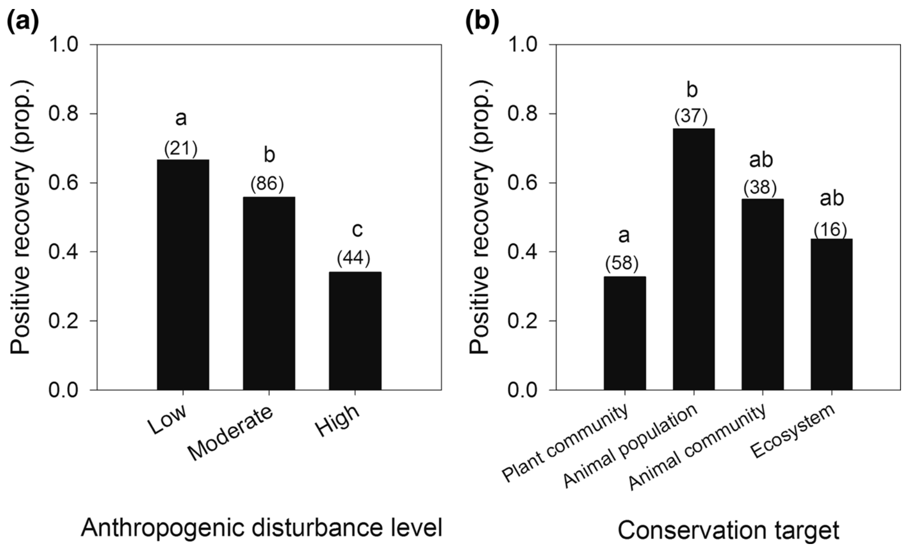


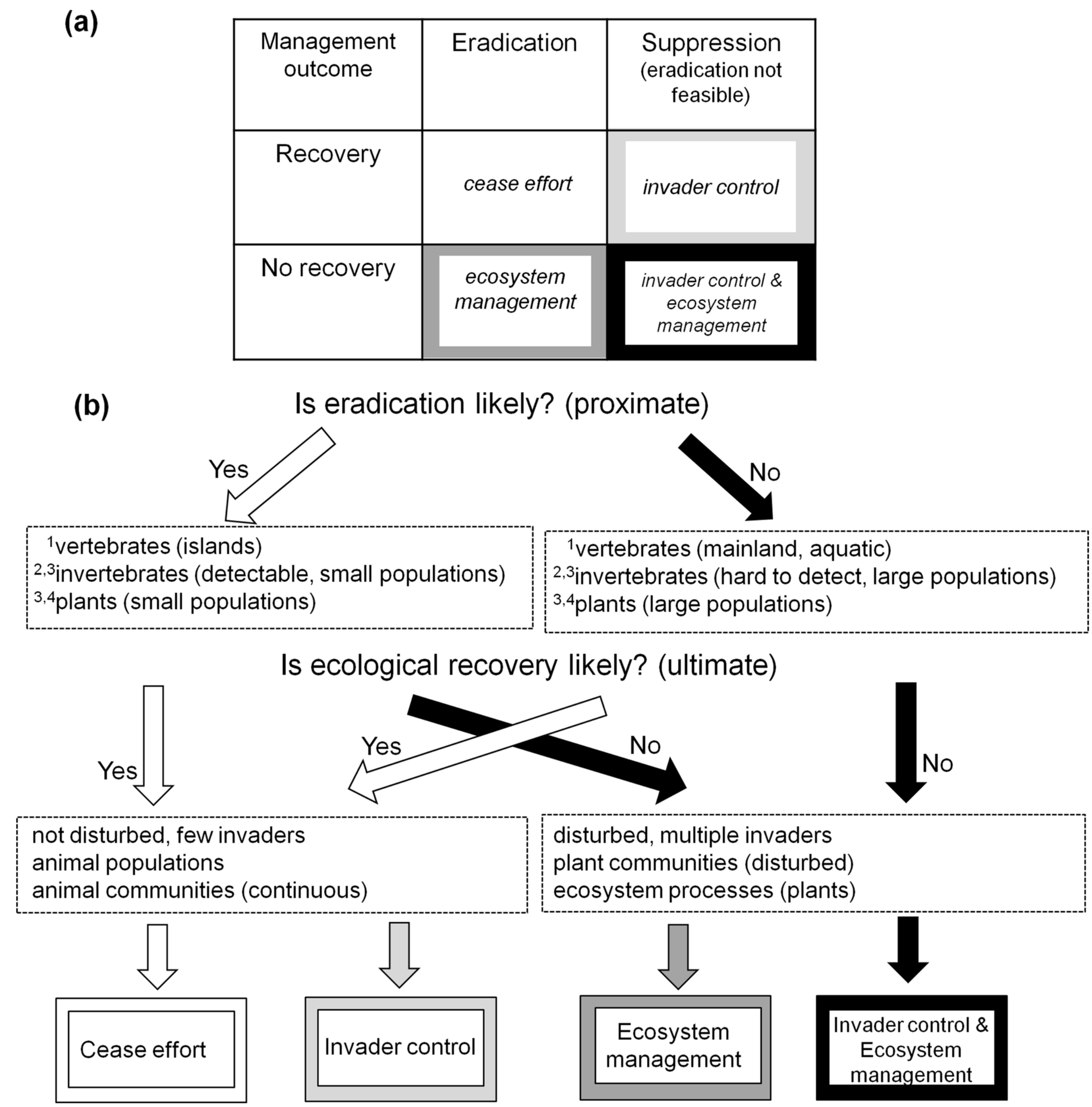
Fig. 3 The proportion of studies in which ecological recovery was positive in **a** low, moderate, or highly disturbed areas; and when **b** plant communities, animal populations, animal communities, or ecosystem processes responded (N = 151 studies). *Numbers* above each *bar* represent the number of studies in each group. *Different letters* represent significantly different groups (Tukey's: $P < 0.05$)

removed in larger management areas ($\chi^2_{1,17} = 20.38$, $P = 0.015$), and when recovery was assessed over longer periods of time ($\chi^2_{1,17} = 20.71$, $P = 0.018$). These factors are all correlated with taxonomic group that was not retained in the final model, but in which positive recovery occurred less when plant invaders were removed compared to animal invaders ($\chi^2_{1,17} = 21.45$, $P = 0.028$). Given that the variables in the final models were correlated with each other and with taxonomic group (Spearman's $R = 0.45$–0.88), it is difficult to tease apart which of these variables are driving patterns in the recovery of ecosystem level processes.

Discussion

Ecological systems are complex, not always resilient, and increasingly altered by environmental change. These complexities mean that ecological systems are not likely to recover in straightforward ways from the alleviation of environmental change such as invasive species (Hobbs and Norton 1996; Zavaleta et al. 2001; Suding et al. 2004; Jones and Schmitz 2009). Despite this, it is still common for invasive species management to focus on managing populations of invasive species and to assume that ecological systems will passively recover (Kettenring and Adams 2011; Suding 2011; Schweizer et al. 2016; Jones et al. 2016). Our synthesis provides insight into how often and in what contexts this assumption holds true. We reveal that clear ecological benefits of invasive species removal occurred in just over half of the studies. Mixed outcomes that are partially positive occurred in another 18% of studies. Thus, in many cases invasive species removal leads to ecological gains and invasive species management is a successful practice. Passive recovery post invasive species management is common because employing additional management is costly (D'Antonio and Meyerson 2002; Prach and Hobbs 2008). However, limited resources may also be wasted when management practices misalign with management goals.

While invasive species removal is successful in many cases, it can also be a failure from the perspective of ecological recovery. In 31% of studies, ecological systems did not recover, or there were negative or unintended consequences. Thus, invasive species management should be viewed as a part of more comprehensive and integrative conservation and restoration strategies (Young et al. 2000; Atkinson 2001; Zavaleta et al. 2001; Zavaleta 2002; Suding 2011; Hulme 2006; Kettenring and Adams 2011). Instead of stopping at invader removal and allowing



for passive recovery, managers should anticipate that in many cases additional management activities will be necessary. Such activities include active management, such as re-populating native species or managing habitats after invader removal or adaptive management, such as responding to unanticipated outcomes (Atkinson 2001; Zavaleta et al. 2001; Zavaleta 2002; Caut et al. 2009; Reid et al. 2009). Pre-management ecological assessments, such as determining the trophic position and diet of the invader, their interactions with other native and exotic species, the extent and potential lasting effects of their impacts, and if they play an important functional role will help to anticipate if and what management might be necessary post-invader removal to recover ecological systems (Atkinson 2001; Zavaleta 2002; Courchamp et al. 2003; Caut et al. 2007, 2009; Buckley and Han 2014). However, pre-management assessments

◀**Fig. 4** **a** Four different management scenarios based on managing for ultimate goals (ecological recovery) and proximate management goals (population-level management). In the first scenario (*white quadrant*) eradication is feasible and ecological recovery occurs. This is the only scenario in which eradication should be viewed as a potentially permanent management solution, in which management efforts can cease. In the second scenario (*dark gray quadrant*), eradication is feasible, but ecological recovery does not occur. In this case, eradication is not a permanent solution given that additional or follow-up management, such as active management or the management of additional invasive species ("ecosystem management"), will be needed to achieve ultimate goals. In the third scenario (*light gray quadrant*), when eradication is not feasible suppression should be implemented. In these cases, resources should not be wasted on trying to eradicate species or find every last individual; however, follow up monitoring and control of the invader population will be necessary ("invader control"). Finally, in the last scenario (*black quadrant*), invader control and ecosystem management will be needed for cases in which eradication is not feasible and ecological systems do not recover. Our synthesis revealed that outcomes of all scenarios (i.e., each quadrant) occurred 21 (*white*), 29 (*dark gray*), 22 (*light gray*), and 28% (*black*) of the time. Thus, management beyond the initial removal of invader populations will be needed for most management programs (in 78% of cases). **b** Our synthesis combined with others on eradication success provides guidance into cases in which each management scenario (**a**) is likely. Several syntheses have revealed that eradication is more likely for certain types of invaders than others, such as vertebrate mammals on islands (Kiett et al. 2011), arthropods that are easy to detect and in small populations (Pluess et al. 2012; Tobin et al. 2014), and in small populations of plants (Rejmanek and Pitcairn 2002; Pluess et al. 2012). In these cases eradication should be implemented. Post-eradication or removal, our synthesis revealed that there are certain cases in which ecological recovery is more likely. By mapping these trends onto our four management scenarios, we can provide guidance into in which cases follow-up management in terms of invader control or ecosystem management are most likely to be needed. For example, we should expect to see high conservation gains of animal populations on islands after invasive mammals have been eradicated (*white quadrant*). However, for animal communities in isolated habitats, or invasive plants managed in highly invaded ecosystems, active or additional management might be necessary for recovery (*dark gray quadrant*). [1]Kiett et al. (2011), [2]Tobin et al. (2014), [3]Pluess et al. (2012), [4]Rejmanek and Pitcairn (2002)

are not always practical or optimal, given that they take time and are costly (Zavaleta 2002; Simberloff 2003).

Also useful to anticipate how to prioritize management efforts is to search for generalizations among past studies to uncover contexts conducive to ecological recovery. Our synthesis revealed that anthropogenic disturbance was the most important factor determining positive recovery, since recovery occurred in 67% of cases in less disturbed habitats such as preserves, but only in 34% in highly disturbed habitats such as urban parks (see Table 2). While invasive species is a leading cause of environmental change, multiple stressors—such as habitat conversion, climate change, and nutrient loading—impact ecosystems. These multiple and interacting stressors can lead to entirely novel ecosystems that might be incapable of converting back to historical states (Hobbs et al. 2006, 2009; Seastedt et al. 2008). Moreover, invasive species can either act as drivers or passengers of environmental change; when invaders are not drivers their removal will not alleviate impacts (Gurevitch and Padilla 2004; MacDougall and Turkington 2005). In one study, Chapuis et al. (2004) found that rabbit eradication on a subantarctic island resulted in widespread invasion by a generalist plant that is also facilitated by climate change. Rodewald et al. (2015) found that bird communities did not respond to honeysuckle removal in urban areas likely because habitat fragmentation precluded recovery. Highly disturbed habitats in our review also included areas that were invaded by multiple invasive species. Increases in other invasive species were common, occurring in 20% of studies. Our results suggest that in heavily disturbed systems, including those with multiple invaders, managers need to plan for managing beyond single invader removals (Zavaleta et al. 2001; Hobbs et al. 2006, 2009; Kettenring and Adams 2011). Alternatively, if invader removal is the only management intention, managers should focus on habitats that are less disturbed by other environmental change stressors.

Conservation target also explained patterns in ecological recovery. Deciding on conservation targets needs to be an integral part of management programs in natural systems and defining appropriate targets is a major topic of discussion in restoration ecology (Bonanno 2016; Suding 2011). Targets can vary widely in ambition and rationale; yet need to be defined clearly given that conservation goals do not always align (Bonanno 2016). For example, increases in biodiversity do not always lead to increases in ecosystem processes or services, and the restoration of one ecosystem service may come at a cost to another (Findlay et al. 2003; Galatowitsch 2009; Buckley and Han 2014). We found that removing invasive species caused large conservation gains for animal populations, more moderate gains for animal communities, and mixed results for plant communities and ecosystem processes. Animal populations experienced positive recovery in 74% of cases. A recent review also found great conservation gains of animal populations on islands with successful animal eradications (Jones et al. 2016). We found a more moderate positive response for animal communities (55%) because, in many cases, only a subset of species in a community recovered. For example, the eradication of rats from the several Falkland Islands increased bird species richness; however, two species of conservation concern failed to recover (Tabak et al. 2014). Plant communities responded only 33% of the time. This result was not unexpected given that plant communities are often heavily invaded, and many removals allowed for increases in other invasive species (Kettenring and Adams 2011; Cole et al. 2012; Schweizer et al. 2016). Finally, ecosystems only recovered 44% of the time. This result is likely because the recovery of ecosystem processes is complicated depending on the restoration of several interacting biotic and abiotic elements (Jones and Schmitz 2009; Suding 2011). Our results suggest that as the conservation target increases in complexity from a population to a community to an ecosystem, managers need to anticipate additional or alternative management to meet conservation goals. Given that goals do not always align, clearly defining conservation goals a priori will help managers employ the most appropriate management actions to meet those goals (Suding 2011; Bonanno 2016).

We predicted that several other characteristics of the invader and invaded community would influence the likelihood of ecological recovery. Trophic level or taxonomic group of the invader can have a strong bearing on impacts (Elton 1958; Lodge 1993; Strayer 2010; Ricciardi et al. 2013). Top invasive predators, for example, have profound consequences being one of the leading causes of biodiversity loss on islands (Clavero and Garcia-Berthou 2005). In turn, predator removal is likely to result in unanticipated effects given their numerous direct and indirect trophic links (Zavaleta et al. 2001; Courchamp et al. 2003; Bergstrom et al. 2009). However, invasive primary producers, herbivores, and omnivores also have substantial impacts on communities and ecosystems (Nunez and Pauchard 2010; Strayer 2010; Bobeldyk and Lamberti 2010; Vila et al. 2011). We did not find an effect of trophic level on the likelihood of ecological recovery. We also predicted that the potential for recovery would be different among ecosystems with larger impacts in simplified systems with strong trophic links (i.e., island or aquatic systems) (Courchamp et al. 2003; Gallardo et al. 2015; Prior et al. 2015b). However, we found no differences in the likelihood of recovery among ecosystems. Finally, we expected that invasive species that had established for an extended period would have greater impacts and in turn their removal leading to low chances for recovery (Zavaleta et al. 2001). Again, we found no effect; this could be a result of little variation in establishment times in our study set.

We also expected that the likelihood of ecological recovery would be influenced by elements of management activities such as if multiple invaders were removed, if the management unit was more continuous or more isolated, the size of the management unit and the time allowed for ecological recovery. However, variation in these management practices did not affect recovery when we analyzed our dataset as a whole. We also predicted that eradication would lead to recovery more than suppression. However, we found that both management practices equally resulted in positive recovery (49 and 51% of cases respectively). This finding has important implications given that eradication is assumed to more completely alleviate impacts than suppression (Myers et al. 1998, 2000; Hulme 2006; Pluess et al. 2012). Eradication (zero population) compared to suppression (low population) is difficult to achieve in many circumstances (Myers et al. 1998; Simberloff 2001; Kiett et al. 2011; Pluess et al. 2012; Tobin et al. 2014), yet it is sometimes stated as the population-level management goal even for some hard to eradicate invasions (Myers et al. 2000; Pluess et al. 2012). Moreover, when eradication is perceived as favorable managers may make decisions not to implement management activities because the bar for success and perception of failure is high (Myers et al. 2000).

Managing for ultimate goals rather than proximate invader population-level goals can lead to more ecologically- and economically- efficient management decisions (Fig. 4). For example, if managing for the ultimate goal of ecological recovery, eradication may not be necessary given that recovery can occur even when 100% of the invader population is not removed (Simberloff 2009). In cases in which eradication is a feasible goal it should be implemented (e.g., for vertebrates on islands, insects that are easy to detect, and when invasions are small and contained) (Kiett et al. 2011; Pluess et al. 2012; Tobin et al. 2014). However, it should not necessarily be perceived as a universal or permanent solution, given that eradicating an invader will not always lead to ecological success (Fig. 4). For species that are difficult to eradicate, managers should not waste time or resources trying to find every last individual (the most expensive portion of an eradication program) because suppression can also lead to ecological recovery (Reid et al. 2009; Kettenring and Adams 2011). Again, follow up management of the invader and additional management should be a part of the planned management activities. Focusing on ultimate rather than proximate goals will lead to a more optimal allocation of limited resources.

There are important caveats to these recommendations. For some species that have compensatory population growth (higher population growth at small numbers) suppression can backfire and thus either eradication or doing nothing is more effective than suppression (Ruiz-Navarro et al. 2013). Also, in some cases, suppression is not as good as eradication at achieving ecological recovery. For example, invasive populations of *Cervus elaphus* (red deer), even at small populations can devastate native tree communities and need to be completely removed to allow for recovery (Tanentzap et al. 2009).

Within each conservation target, we found some general patterns in factors that allow for ecological recovery. Animal communities had a greater recovery in more continuous than in more isolated management units because recovery was likely facilitated by recruitment from neighboring locations. Buxton et al. (2014) found that distance to source population was the greatest predictor of the recolonization of seabirds post rat eradication on islands in New Zealand. Thus, active management of animal communities should be prioritized in isolated areas. Plant communities had low ecological recovery in highly disturbed or heavily invaded sites. This was largely due to increases in other invasive species, and managing multiple invasive species should be an integral part of managing invaded plant communities (Zavaleta et al. 2001; Reid et al. 2009; Kettenring and Adams 2011). Finally, several factors were important in determining the likelihood of ecological recovery at the ecosystem level. Recovery was more likely in systems in which the invader was eradicated versus suppressed, removed over large areas, and assessed over a long time period. All of these factors were correlated with each other, and with trophic level, so it is difficult to tease apart which factors are important in facility the recovery of ecosystem processes.

Our comprehensive review builds on the seminal review by Zavaleta et al. (2001). We capitalized on the studies published since this review, focusing on studies in the published literature. There are likely many more cases in the "gray literature" in which data has not been formally reported or published in the reviewed, indexed literature and adding these cases would likely strengthen our results. However, collecting gray literature data comprehensively would be challenging and is beyond the scope of our current study. While adding studies from the gray literature might strengthen our results, our data set provides a robust set of cases with wide coverage that includes the invaders in which there have been significant management effort and the most quantitatively rigorous ecological assessments.

Measuring the success of a management program is challenging, and often debated. We measured ecological outcomes at the study level if recovery was moving towards the conservation target or not and view this as an accurate way to score success because the authors made conclusions or recommendations often based on known management goals. We chose the four outcomes based on commonly reported outcomes of restoration programs (Suding 2011) and scored the outcome as positive removal led to an ecological improvement relative to the invaded state. Another way to score the success of a management program is to compare managed sites to "baseline" uninvaded sites. Only a small subset of our studies included a baseline treatment. As well, achieving conservation goals by restoration to an ecological baseline is difficult given that baselines often change and returning to some point in the past is in many cases unrealistic or not useful (Parker et al. 1999). Finally, the length of time in which ecological recovery was measured was short in some cases. Thus, our estimates of recovery may be underestimated because some systems could take decades or longer to recover (Jones and Schmitz 2009). Alternatively, recovery could be reversed, especially for suppression programs in which invader removal might not be permanent (Myers et al. 1998; Kettenring and Adams 2011; Pluess et al. 2012).

Conclusions

The growing numbers of species and ecosystems threatened by invasive species, combined with limited or decreasing resources for conservation, forces managers to consider not only the intrinsic value of their targets, but also the economic costs of programs. In an increasing number of cases, economics dictates which species or ecosystems will be protected and the scope of actions that are implemented. Funding for invasive species management activities is sometimes allocated in piecemeal units and may not often be linked to restoration or conservation funding. This type of funding strategy is often why population-level management, with the assumption that removal passively leads to conservation gains, is a popular approach to managing invaded natural ecosystems. Managing for ultimate rather than proximate goals and taking integrative approaches to managing invaded ecosystems with clear targets and assessments of outcomes may allow for more economical and effective management of natural ecosystems.

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