

Functional eradication as a framework for invasive species control

Stephanie J Green^{1*} and Edwin D Grosholz²

Invasive species continue to drive major losses in biodiversity and ecosystem function across the globe. Dealing with the effects of invasion is particularly problematic in marine and freshwater habitats, because the pace at which invaders establish often greatly outstrips the resources available for their eradication. While most managers in North America now focus on ongoing containment and suppression interventions, they often lack quantitative guidance from which to set targets and evaluate success. We propose practical guidelines for identifying management targets for invasions for which eradication is unfeasible, based on achieving “functional” eradication – defined as suppressing invader populations below levels that cause unacceptable ecological effects – within high-priority locations. We summarize key ecological information needed to inform this strategy, including density–impact functions and recolonization rates. We illustrate the framework’s application for setting local suppression targets using three globally invasive species as examples: red lionfish (*Pterois* spp), European green crab (*Carcinus maenas*), and rusty crayfish (*Faxonius rusticus*). Identifying targets for suppression allows managers to estimate the degree of removal required to mitigate ecological impacts and the management resources needed to achieve sufficient control of an invader.

Front Ecol Environ 2021; 19(2): 98–107, doi:10.1002/fee.2277

More than 60 years after the unintended consequences of species introductions were first formally recognized (Elton 1958), addressing the negative effects of invasions remains a top challenge for conservation. Biological invasions threaten ecosystem structure and function globally, and

continue to expand in both frequency and geographic extent (Mooney and Cleland 2001). The ecological impacts of invaders include predation-mediated extirpations and extinctions of native prey (Witte *et al.* 1992; Hadfield *et al.* 1993), exclusion of native competitors (eg Sax and Gaines 2008), and changes to fire regimes and nutrient cycling (D’Antonio and Vitousek 1992), among others. These ecological changes often interrupt the flow of nature-derived goods and services to people, causing substantial socioeconomic impacts (Pechar and Mooney 2009).

Population control – typically via removal of individuals from invaded habitats – is the current strategy most commonly used to manage ecological and economic harm of invasive species (Figure 1; Epanchin-Niell and Hastings 2010). However, population control often requires substantial amounts of resources and time, limiting the spatial and temporal scale of control efforts (Zavaleta *et al.* 2001). Consequently, population control leading to eradication from the invaded range is closely linked to invader population size, the geographic extent of spread, and the ease of locating and removing the invader (Myers *et al.* 2000; Simberloff 2009).

Mitigating the effects of invasion is especially problematic in marine and freshwater habitats, because the pace at which invaders establish and spread in these systems often outstrips the resources available for their eradication. Aquatic habitats cover more than 70% of the planet, and many aquatic organisms disperse broadly, propelled by water- and wind-driven currents (Kinlan and Gaines 2003). In addition, humans have limited access to aquatic environments because of depth restrictions. Consequently, many aquatic invasive species (AIS) can become widely distributed before they are detected.

The challenge of managing AIS is highlighted by the responses of 232 managers and AIS specialists in the US and

In a nutshell:

- Eradicating aquatic invasive species is rarely practical, and most managers in North America now focus on containment and ongoing population suppression
- Quantitative targets for suppression activities are essential for defining intervention success and efficiently allocating limited management resources, but are typically not available
- We outline a framework in which managers can apply monitoring data to identify targets for density suppression that efficiently minimize ecological impacts in high-priority habitats by achieving local “functional eradication”
- The necessary data include relationships between invader densities, change in affected ecosystem components, and recolonization rates, information that could be obtained from monitoring programs underway for many high-priority invasions
- Examples of the practical application of a functional approach are presented to illustrate how the framework can be broadly applied across invasions and locations

¹Department of Biological Sciences, University of Alberta, Edmonton, Canada* (stephanie.green@ualberta.ca); ²Department of Environmental Science and Policy, University of California–Davis, Davis, CA

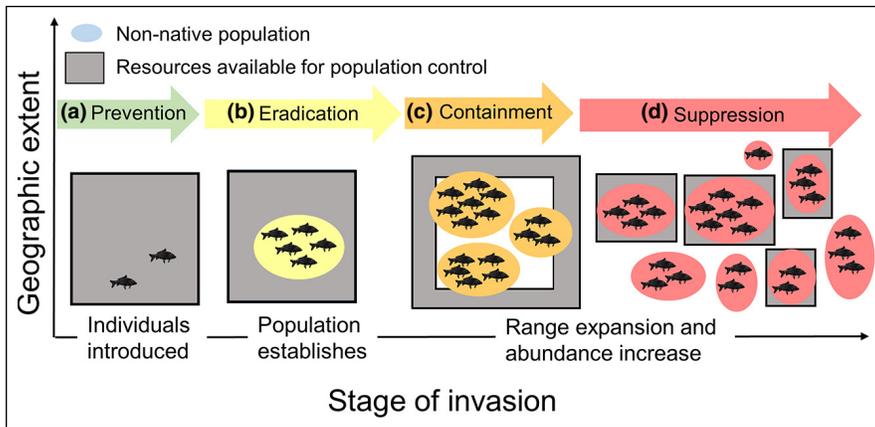


Figure 1. Relationship between stage of invasion, geographic extent, and management resources available for intervention. Total resources (personnel, funding, equipment) for population control are limited, necessitating their effective allocation in accordance with the goals of management intervention. For early stage invasions with small geographic ranges (a) preventing establishment and (b) achieving complete eradication may be possible with available resources. (c) In the case of invasions for which invasive population distribution is greater than the resources needed to achieve complete eradication, resources may be allocated to extirpation at the range edges to prevent further spread. (d) For widespread invasions, resources could be allocated to suppressing populations in high-priority habitat locations via a functional eradication approach (Figures 3 and 4) based on such criteria as probability of recolonization and the vulnerability of the ecological community to invasion impacts.

Canada to a recent online survey conducted in partnership with the regional panels of the US Aquatic Nuisance Species Taskforce. Respondents reported that nearly 80% of priority marine and freshwater invaders were spreading beyond their management jurisdiction, precluding complete eradication (Figure 2). For established or geographically expanding AIS, management activities are now primarily focused on suppressing population densities (57% of marine and 21% of freshwater invasions; Figures 1d and 2) or containment (21% of marine and 40% of freshwater invasions; Figures 1c and 2) rather than eradication (0% of marine and 11% of freshwater invasions; Figures 1b and 2).

Despite this focus on strategies intended to reduce (rather than eliminate) invasive populations, few managers surveyed (2%) identified quantitative targets or criteria to evaluate the magnitude of population control needed to achieve sufficient suppression (Figure 2). Moreover, most research devoted to invasive species control focuses on estimating the mortality required to achieve population decline and ultimately eradication (Taylor and Hastings 2004). These observations suggest that while suppression-based strategies are a priority for managers, there is a major gap in the information and decision-making tools needed by managers engaged in AIS control to guide suppression activities. For invasions unlikely to be eradicated with available management resources, two major conservation science questions arise: (1) what level of control is sufficient to mitigate ecological impacts in high-priority management areas, and (2) what resources are required to achieve a sufficient level of control? Addressing both questions requires linking quantitative estimates of impact on recipient ecosystems with invader

population densities and repopulation rates, information that is urgently needed to guide the population suppression required to achieve and sustain ecological benefits.

Ecologically relevant management targets

There has been considerable recent focus on quantifying the consequences of biological invasions and characterizing common features of high ecological impact (Vander Zanden *et al.* 2017). However, less attention has been paid to developing practical guidelines for managing high-impact invaders in places where eradication is unfeasible. Our main objective is to outline practical guidelines for population suppression by switching the focus from “numerical eradication” – defined as complete extirpation from the invaded range – to “functional eradication”, which we define as reducing local densities below levels that cause unacceptable effects on recipient ecological communities in high-priority habitats. The concept of suppress-

ing a species below a threshold of economic impact has been applied to many pest invasions (Gren 2008), including forest pests (Liebhold *et al.* 2016) and agricultural systems (ie “damage functions”; Power 2010; Letourneau *et al.* 2011). Although there are examples of successful eradication (Simberloff 2001; Liebhold *et al.* 2016), suppression continues to be the most common strategy for most agricultural pests. Conservation scientists also increasingly recognize the need to deduce numerical relationships between invasive populations and their ecological impacts (ie density–impact functions; Green *et al.* 2014; Norbury *et al.* 2015). However, despite substantial information on the impacts of many invaders, a general framework for linking forms of the density–impact relationship to explicit management decision making must be developed and tested for practical application.

We propose that functional eradication could be achieved in three broad steps: (1) quantification of the mechanisms by which invaders negatively affect native communities (ie predation, competition, habitat engineering, and so forth); (2) identification of invasive population levels that elicit unacceptable effects (ie identifying the shape and magnitude of density–impact functions); and (3) combining the products of steps (1) and (2) with data on repopulation rates following suppression. When unacceptable ecological effects are likely and invaders are broadly distributed, shifting the management focus to “functional eradication” should result in more efficient allocation of resources (Figure 3). Resources that would be allocated to complete extirpation (with little added ecological benefit; Figure 3b) could be applied to a wider geographic area over which invaders are suppressed below target densities

(Figure 1d), an advantage for conservation practitioners seeking to efficiently allocate resources across their jurisdiction.

Information needs to design functional eradication

To practically implement functional eradication, practitioners must define “unacceptable” change in the recipient ecosystem (Figure 3a) and determine the resources required to sustain suppression of invasive populations below levels that cause this damage (Figure 3b). We suggest that this process can be achieved by quantifying and linking together of two relationships: (1) ecological change as a function of invader population density and (2) invader population density as a function of removal intensity.

Relationship between invader density and change in ecosystem components

The shape of the relationship between population density and ecosystem response (ie density–impact function) will vary among invasions (WebFigure 1) based on several factors, such as the (1) types of ecological interactions between native and invasive taxa (eg predation, competition, ecosystem engineering); (2) life-history characteristics of the invader, which influence population increase and spread; and (3) initial state of the ecosystem. Although numerous types of density–impact relationships are possible (WebFigure 1b), theory and empirical data suggest that non-linear relationships are most prevalent in many environments (Figure 3a; Suding and Hobbs 2009). Observed threshold dynamics stem from non-linear population processes, including reduced population growth rate at large population sizes (eg resource competition), decreases in population growth rate at small population sizes (eg Allee effects), and limits on rates of resource acquisition in relation to resource density (ie Type I and II functional responses; Suding and Hobbs 2009). Non-linear relationships, and in particular those characterized by a declining exponential function, appear to be most common for terrestrial invasions (Norbury *et al.* 2015). Research to date on aquatic invaders in the context of functional responses clearly shows strong support for the prevalence of non-linear density–impact relationships, commonly in an exponential Type II form (Dick *et al.* 2017; Laverty *et al.* 2017). In cases where non-linear dynamics prevail, managers can assess return on investment in terms of ecological benefit gained per unit of density reduction achieved

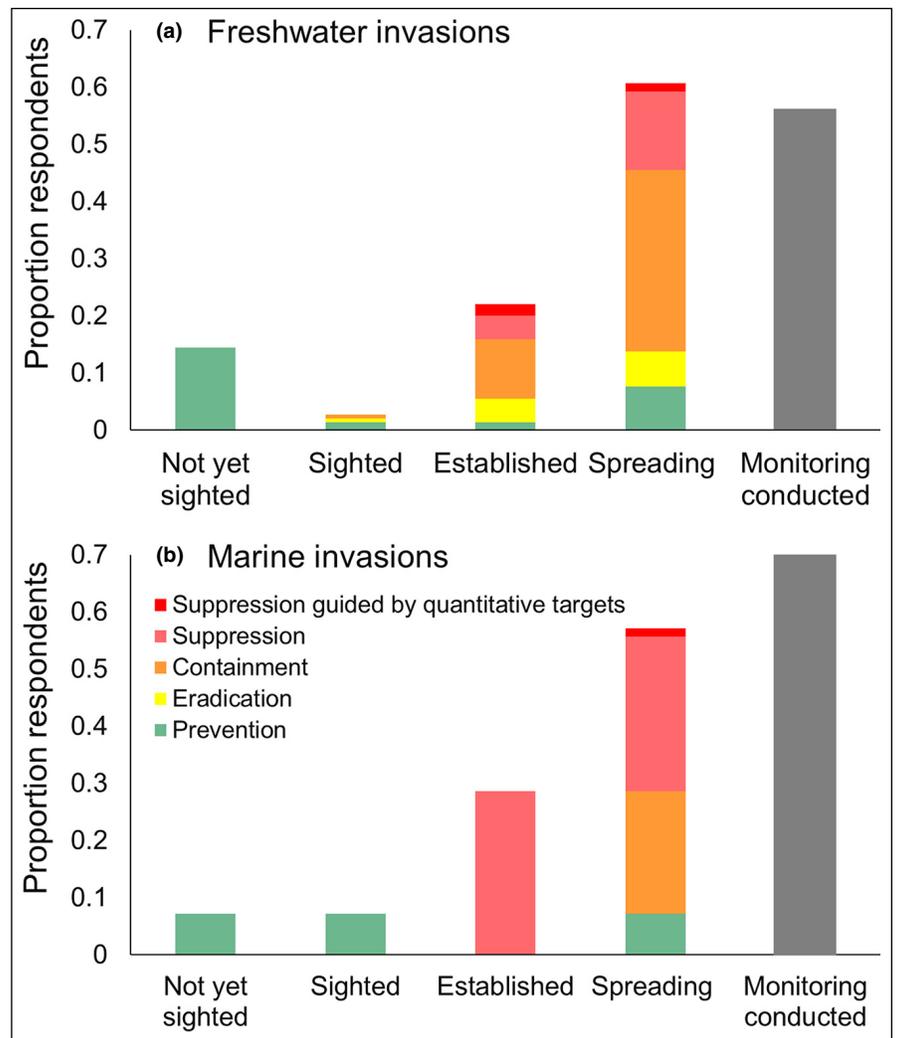


Figure 2. Relationship between the proportion of North American aquatic invasive species (AIS) managers' intervention goals and the status of high-priority invasions in their jurisdiction ($n = 232$ respondents) for (a) freshwater invasions and (b) marine invasions. Gray bars represent the proportion of respondents indicating that monitoring data on invader populations and ecological changes/impacts were being gathered for high-priority invasions in their jurisdiction; red shading indicates proportion of suppression-based activities guided by quantitative targets.

(Figure 3), a property supported by modeling and empirical tests (Figure 3b; Baxter *et al.* 2008; Green *et al.* 2014).

Relationship between invader density and recolonization following control

Rates of invader recolonization following population control are driven by both recruitment (ie new individuals via reproduction) and immigration from surrounding habitats (WebFigure 1a). Non-linear dynamics have been demonstrated in many aquatic organisms, with implications for suppression-oriented population control. For example, allocating effort to reduce invasive populations below thresholds at which Allee effects (common in aquatic invertebrates; Kramer *et al.* 2009) occur may reduce future repopulation

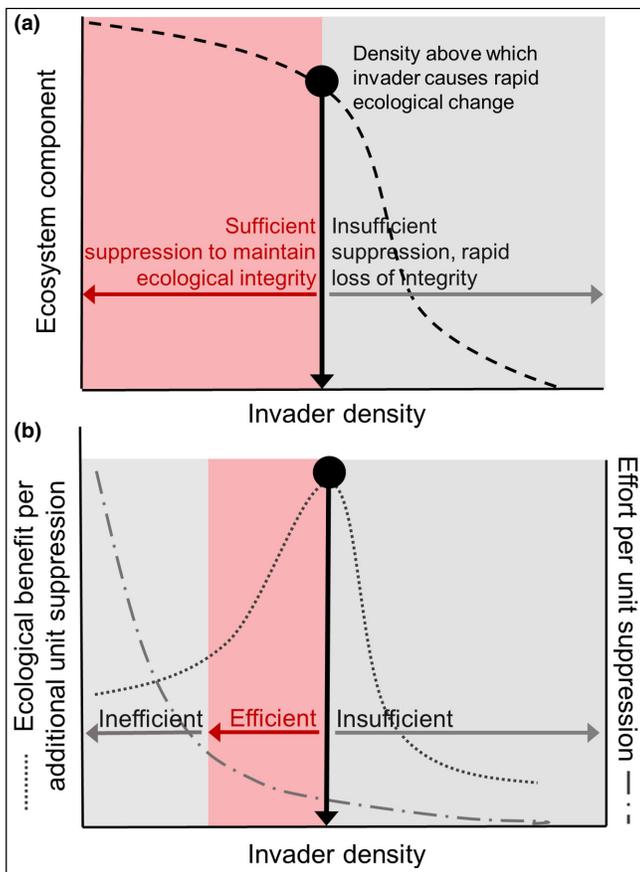


Figure 3. Functional eradication achieved by (a) identifying population densities at which invaders elicit major change in the recipient ecosystem (ie density–impact function) and (b) identifying the range of densities at which the efficiency of suppression effort is maximized.

rates without the need for additional interventions (WebFigure 1a). Other well-known density-dependent processes that can inform management targets include negative population growth at high densities (ie stimulated via resource limitation and competition) and rapid population growth at low densities, a feature described in fisheries models (WebFigure 1a; Abrams and Matsuda 2005). Although rapid population growth at low densities can be used in conservation contexts, such as attempts to prevent species extinction (Suding and Hobbs 2009), increased reproductive success and population growth at low adult densities (ie “overcompensation”) can undermine suppression efforts for invasive species (curves i–iii in WebFigure 1c; Weidel *et al.* 2007). Therefore, overcompensation may determine a useful and important lower limit for population suppression of aquatic invaders.

■ Functional eradication in practice

Harnessing research and monitoring data on ecological change

A precursor to designing functional eradication is identifying which components of the recipient ecosystem will be most

affected by an invasion. Ecological hypotheses about the sensitivity of ecosystem components can be generated from insights into the functional role of the invader in its native range, which may illuminate categories of strong interactions in a new ecological context (eg competition, predation, habitat engineering). Studies of functional traits within recipient ecosystems, in relation to the traits of invaders, have yielded promising insights into the species most likely to be strongly affected without having the need for observable impacts (Kimbro *et al.* 2013). However, a priori vulnerability assessments are rarely performed, and vigorous ecological interactions with native species in the invaded system are often revealed through observations of decline, prompting the necessity of management efforts. Nevertheless, both existing empirical data documenting decline and mechanistic models of invasion effects can be used to elucidate the shape of the density–impact curves, and will fill the gap that exists in quantitative targets available to guide ongoing suppression-oriented management (Figure 3).

In designing density–impact studies and monitoring, information about ecological change along gradients of invader density is essential for identifying non-linear dynamics. In practice, there may be a range of invader densities over which ecological impacts can be measured. Using a range of densities that reflect real environmental variation ensures that ecological dynamics are resolved at a scale relevant to management. For example, studies focused on documenting native species declines at extreme invader population densities may mask resistance to change by native biota at moderate to low invader densities, which are more realistic for management (eg invasive red lionfish [*Pterois* spp; Figure 4a] densities used in Benkwitt [2015] versus Figure 5, a and b).

The concept of intentionally “leaving some behind” via culling activities may be a challenging paradigm shift among invasive species managers and stakeholder groups engaged in AIS removal. Nevertheless, numerous studies of culling activity suggest that removal efforts are often incomplete, and that effort per unit suppression spikes at low invader population densities (Taylor and Hastings 2004). Given this reality, designing monitoring and research with gradients in mind could yield major benefits for deriving ecologically meaningful targets for long-term suppression of invaders that have become widely distributed (Baxter *et al.* 2008). Data on impacts must also be integrated with information on methods (ie tools and techniques) available to suppress an invader, and the costs for these methods (see section entitled “Likely and unlikely conditions for success” below).

Integrating data on local invader population dynamics

The frequency of removal needed to achieve and maintain control targets over time will largely depend on region-specific invader population densities and rates of recolonization following removal. Rates of recolonization are driven by both recruitment (ie addition of new individuals via



Figure 4. Three widely distributed AIS for which a functional eradication approach to population suppression is a relevant strategy based on their current population status in their invaded ranges (Panel 1): (a) red lionfish (*Pterois* spp) in the Western Atlantic, (b) European green crab (*Carcinus maenas*) on the Atlantic and Pacific coasts of North America, and (c) rusty crayfish (*Faxonius rusticus*) in freshwater habitats throughout North America.

reproduction) and dispersal (ie immigration) of individuals from surrounding habitats. Gathering spatially explicit data on recolonization rates following removal in tandem with information about ecological impacts is essential for estimating targets for suppression that account for variation in the structure of local invasive populations and their connectivity across aquatic habitats. Managers can harness insights into the relationship between AIS repopulation rates and habitat type, native biotic community composition, and initial invader density to allocate management effort to areas where they are most likely to achieve and maintain functional eradication targets. Tracking management resource use (eg visit frequency, personnel, and equipment) as a function of AIS target density and recolonization rates would allow managers to gauge the efficiency of their strategy (eg Baxter *et al.* 2008). Selectively harvesting particular stages/ages of an invasive population may also yield benefits in terms of minimizing repopulation rates and maximizing ecological benefits. For example, ecological effects from invasive red lionfish and rusty crayfish (*Faxonius rusticus*; Figure 4c) are influenced by body size and sex, respectively (Figure 5, a, b, e, and f). Removal focused on large size classes or females may yield benefits in terms of reducing propagule pressure in areas with local recruitment (ie self-seeding habitats; Panel 1; Figure 5, c and d).

Design and analysis considerations

The accuracy of targets for suppression derived from density–impact and density–repopulation functions is likely to depend on the extent to which data for both relationships are gathered for similar time periods and geographic regions. In addition, the precision of suppression targets is influenced by the methods used to estimate density–impact and density–recolonization relationships. Ideally, sampling methodologies would be standardized across data collection efforts so that they generate directly comparable estimates of invader population density, using approaches for which sampling bias and measurement errors have been estimated. Once the necessary data are in hand, many analytical approaches exist for assessing the shapes of the relationships between

diverse ecological variables and, for non-linear relationships, estimating the position of key thresholds that are directly useful for management intervention (Andersen *et al.* 2009).

■ Likely and unlikely conditions for success

Encouragingly, most of the Canadian and US AIS managers surveyed indicated that monitoring data on both invasive populations *and* their ecological effects are being gathered for priority invaders within their jurisdictions (70% of marine invasions; 57% of freshwater invasions; Figure 2), highlighting an opportunity to shift monitoring methods and analyses in such a way that they can be used to gather the information needed to estimate targets for suppression via a functional eradication approach. When empirical data (Figure 5) are applied to the conceptual model we outline here (Figures 3 and WebFigure 1), characteristics that make some invasions more suited to a functional eradication management approach than others become apparent. In particular, functional eradication is best suited to invasions that involve a clear and dominant mechanism of ecological impact to the recipient system and non-linearity in the density–impact function (Figure 3; curves vii and viii in WebFigure 1c). Many predatory invaders may be excellent candidates for functional eradication, as prey consumption is often governed by density-dependent (ie non-linear) dynamics. In addition, functional eradication is most appropriate for invasions where Allee effects are operating, such that reduction below a certain threshold could lead to further invader decline (curves iv and v in WebFigure 1c). There are many other important invaders that could be considered within the functional eradication framework. For example, species such as the invasive bivalves *Corbicula fluminea*, *Potamocorbula amurensis*, and *Dreissena polymorpha*, and the invasive plant *Phragmites australis*, are well studied, have major (and likely non-linear) impacts across trophic levels, and would be difficult to eradicate.

Several attributes of the recipient ecosystem's configuration would support the success of functional eradication. Quantifying spatial variation in the ecological vulnerability

Panel 1. Candidate invaders for functional eradication

Data on ecological effects and recolonization as a function of population density reveal the identity of aquatic invasive species that are likely candidates for functional eradication.

Red lionfish (*Pterois* spp; Figure 4a) have rapidly invaded >4,000,000 km² in the tropical Western Atlantic (Côté *et al.* 2013). Populations are mainly controlled via manual removal with spear, hand nets, and traps (Akins 2012). Of primary concern are non-linear predation impacts to coral reef fishes (Green *et al.* 2012; Albins 2015), likely due to compensatory production by prey species (Figure 5a; Green *et al.* 2014). Field studies and empirical modeling confirm that low densities of lionfish do not elicit strong declines in prey populations (ie resistant density–impact curve). Recruitment is overcompensatory (Figure 5b), suggesting that maintaining at or below ~25 lionfish per hectare could prevent predation-induced declines in native fishes and result in low rates of recolonization (similar to curve iv in WebFigure 1c).

European green crabs (*Carcinus maenas*; Figure 4b) have invaded five continents including the Atlantic and Pacific coasts of North America (Yamada 2001). Of primary concern are non-linear effects of predation on benthic communities (Grosholz 2005) and bivalve aquaculture (Grosholz *et al.* 2011; Beal *et al.* 2016). Reducing green crab populations

via trapping is the main approach for limiting ecological and economic impacts (Figure 5c; Grosholz *et al.* 2011). Lowering adult green crab to a CPUE < 5 can result in strong recruitment due to reductions in cannibalistic adults (Figure 5d). These data indicate that suppressing European green crabs to levels equivalent to a CPUE of 10–20 could minimize economic and ecological impacts and avoid overcompensatory recruitment.

Rusty crayfish (*Faxonius rusticus*; Figure 4c) have established in freshwater habitats throughout North America, where they are mainly controlled through trapping and enhancement of predatory fishes (Hein *et al.* 2007). Of primary concern are the non-linear effects of predation by rusty crayfish on native invertebrates, and competition with native crayfishes (Olden *et al.* 2006; Twardochleb *et al.* 2013). Field studies reveal that ecosystem components are variably sensitive to predation effects (Figure 5e; Wilson *et al.* 2004) and that stock–recruitment dynamics are likely linear (Figure 5f; Hansen *et al.* 2013), suggesting that maintaining rusty crayfish at or below ten individuals per trap could greatly reduce declines in impact-resistant native fishes like bluegill (*Lepomis macrochirus*; ie curve vii in WebFigure 1c), and less than three individuals per trap could reduce declines in more vulnerable native fishes like the pumpkinseed (*Lepomis gibbosus*; ie curve ix in WebFigure 1c).

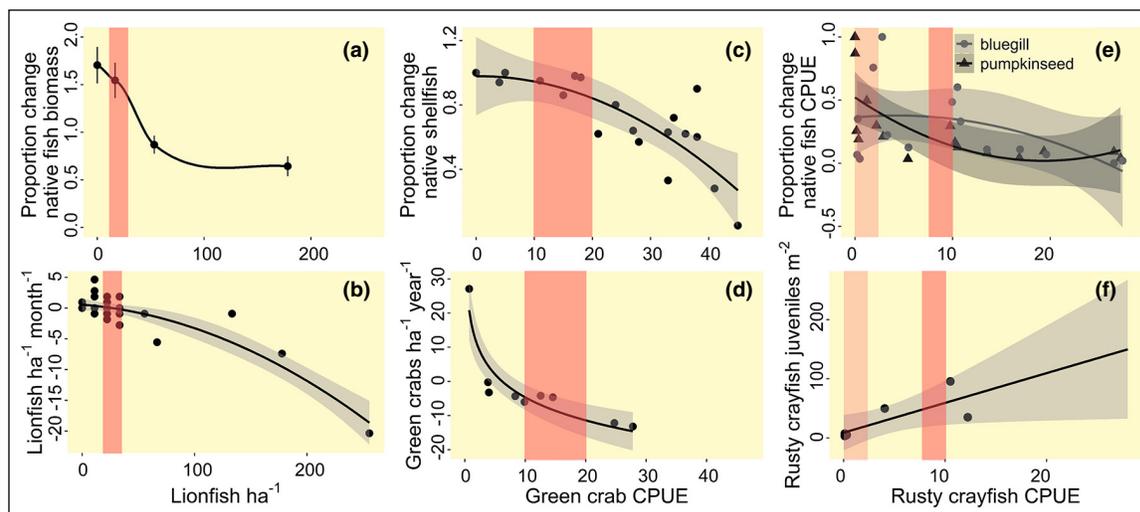


Figure 5. Three examples of applying data on ecological effects and recolonization as a function of invader population density to identify functional eradication targets for suppression. See Panel 1 for case study details. (a and b) red lionfish in the Western Atlantic, (c and d) European green crab on the Atlantic and Pacific coasts of North America, and (e and f) rusty crayfish in freshwater habitats throughout North America. Light red shading in panels (e) and (f) indicates functional eradication targets focused on mitigating ecological change in vulnerable native pumpkinseed (*Lepomis gibbosus*) populations, while darker red shading indicates targets focused on relatively more resilient native bluegill (*Lepomis macrochirus*) populations. Error bars in (a) represent 95% confidence intervals; black lines and surrounding gray regions represent mean and 95% confidence intervals.

(and conversely, resistance) of the recipient ecosystem would allow managers to identify areas of high conservation value in which to prioritize limited management resources. Resistance to impacts is likely dependent on the ecosystem state prior to invasion, which is influenced by other stressors (ie habitat degradation, exploitation, and so forth). Where invasion impacts

manifest via the same mechanisms as past stressors, local biota may resist invasion impacts because sensitive species are already rare (curves i, iv, and vii in WebFigure 1c). However, if invasion affects ecosystem components that are resistant to high levels of other stresses, the recipient system may be exceptionally sensitive to invasions (ie curves iii, vi, and ix in

WebFigure 1c). Finally, habitat heterogeneity (ie patchiness) may greatly influence invader dispersal, affecting both recolonization following removal and population connectivity with adjacent populations not subject to management.

Conversely, there are likely to be situations where functional eradication is less likely to achieve sustained ecological benefits with available management resources: for example, when ecosystem components are highly sensitive to invaders *and* the invader enjoys high rates of density-dependent recruitment and immigration that outstrip the pace of suppression activities (curves iii and vi in WebFigure 1c; eg rusty crayfish, Figure 5, e and f). In such cases, ecosystem components may be better protected by identifying isolated habitats where invader population connectivity and recolonization rates are low in which to maintain complete extirpation of the species. In systems dominated by linear dynamics or where the shape of the density–impact function is unknown, managers must select targets for suppression based on other criteria (curve viii in WebFigure 1c): for example, by linking declines in native ecosystem components or invader density to socioeconomic values (eg fisheries harvest opportunities or reduction in recreational opportunities by aquatic weeds).

An additional complication is the potential for indirect effects of invader suppression on other species, including threatened or endangered species in the same habitat. For instance, removal of tamarisk (*Tamarix* spp) along riparian corridors in the southwestern US has raised concerns about potential loss of southwestern willow flycatcher (*Empidonax traillii extimus*) habitat (Dudley and Bean 2012). However, such complications have rarely been demonstrated in aquatic systems.

■ Considerations

Potential for system hysteresis

The data needed to devise functional eradication targets for suppression include density–impact curves, density–recolonization rates, and estimates of spatial variation in ecosystem vulnerability and invader recolonization. Where such data are available, a key unknown is whether ecosystem recovery generated by invader suppression will follow the same trajectory as the initial decline. The potential for “path dependence” (hysteresis) has been hypothesized and empirically demonstrated in a number of ecosystems as they recover from disturbance or stress (eg Filbee-Dexter and Scheibling 2014). However, the extent to which hysteresis occurs during recovery from invasion is largely undetermined (eg Marchi *et al.* 2011). Documented attempts to remove and eradicate invasive species do not always produce expected ecological recovery (Prior *et al.* 2018), with the magnitude of realized recovery affected by the presence of other anthropogenic disturbances and multiple invasions. The practical implications of hysteresis are that far greater suppression (ie invader density reduction) may be required to return

an ecosystem to its original state than estimated from a density–impact curve constructed from observations of initial decline. Evaluating conditions under which hysteresis occurs requires management experiments that track the effectiveness of functional eradication in practice.

The “where” and “how” of functional eradication

Our framework primarily focuses on the practical quantification of functional relationships between invader density, invader recolonization rates, and ecological change to set targets for ongoing population suppression. As managers identify appropriate interventions for priority invasions (Figure 6), this approach serves as a guide when selecting “how much” suppression is required to achieve desired ecological outcomes. However, “where” and “how” to suppress a given invasion are related problems that must be addressed simultaneously. Numerous tools are available to conduct population suppression, the selection of which will depend on the features of the invader (eg a vertebrate, an alga), the environment (eg small stream, open ocean), and who is conducting the removal (eg natural resource management staff, volunteers from a non-profit organization). In cases where long-term suppression (rather than extirpation or eradication; Figure 6) is the goal, access to quantitative targets derived from a functional eradication approach could help managers evaluate the potential outcomes of engaging stakeholders in alternative methods of population control that generate social and economic benefits. For example, such targets could be considered within bio-economic or fisheries models that predict the contexts in which permitting invasive species harvest achieve suppression of ecological effects and beneficial supplemental income (eg coupled social–ecological model of red lionfish for Belize [Chapman *et al.* 2019]; social–ecological model for eradication that could be adapted for functional eradication [Lampert *et al.* 2014]).

We have discussed the spatial allocation of resources to target locations that minimize recolonization rates following suppression, and that are either more or less vulnerable to invasion effects. The spatial allocation of resources will likely rely on insights into the resources (personnel, financial, and material) required to employ a given strategy and the spatial extent of that strategy. A full treatment of these aspects of devising suppression plans is beyond the scope of this review; however, data on invader density, ecological change, and recolonization rates used to identify functional targets for suppression can be integrated efficiently (ie suppression per unit area per dollar) within optimization functions that identify priority locations for control based on these inputs. Optimization routines are emerging to identify priority locations for conservation action to sustain threatened species (Schuster *et al.* 2019), and their application could easily be adapted using the data discussed here to design invasive species suppression.

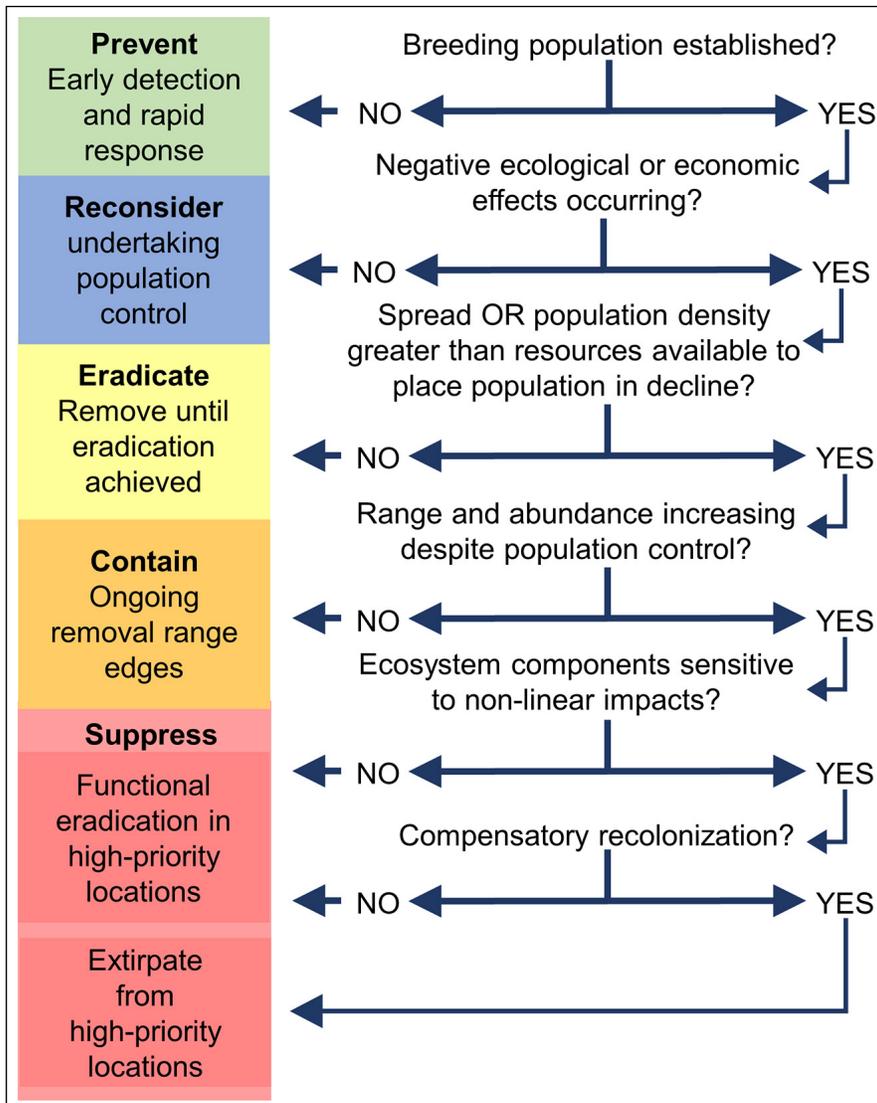


Figure 6. Quantitative decision framework for selecting appropriate management interventions for AIS and integrating guidance on a functional eradication approach to suppression. Decision steps are based on the biological, ecological, and geographic characteristics of the invasion and resources available for control.

Conclusion

Invasive species remain a major threat throughout the world's ecosystems (Mack *et al.* 2000). While eradication can and has been achieved for some invasions (Myers *et al.* 2000; Simberloff 2001), many invasions are occurring at speeds and magnitudes that outstrip the resources available for elimination. Of course, prevention of new invasions is recognized as a top priority and the most cost-effective management strategy, but many invasions are already well underway. In these instances, resource managers and conservation practitioners have two options: do nothing or take action. Developing quantitative targets and evaluating the success of suppression has rarely been part of the conceptual and empirical research along the spectrum of decision making concerning invasive species management (Figure 6). The

practical framework for functional eradication presented here can be used to identify effective and efficient mitigation of the effects of invasive species within areas of high conservation value through the devising of quantitative indicators that link invader density to ecological effects. Consequently, our functional eradication framework addresses the urgent need for conservation action in situations involving high-priority invaders, but in a way that achieves the greatest conservation benefit with the best possible use of available management resources.

Acknowledgements

This research was supported through funding from the David H Smith Fellowship program, and Natural Sciences and Research Council of Canada Discovery and Banting Fellowship grants to SJG. We thank the US Aquatic Invasive Species Taskforce and Regional Aquatic Invasive Species Panels for assistance in the design and dissemination of the managers' survey, N Pentyluk for assisting in assembling the resulting survey data, and Stuart Coves Dive Bahamas, and D Watkinson (Fisheries and Oceans Canada) for images used in Figure 4.

References

- Abrams PA and Matsuda H. 2005. The effect of adaptive change in the prey on the dynamics of an exploited predator population. *Can J Fish Aquat Sci* **62**: 758–66.
- Akins JL. 2012. Methods for control. In: Morris Jr JA (Ed). *Invasive lionfish: a guide to control and management*. Ft Pierce, FL: GCFI Press.
- Albins MA. 2015. Invasive Pacific lionfish *Pterois volitans* reduce abundance and species richness of native Bahamian coral-reef fishes. *Mar Ecol-Prog Ser* **522**: 231–43.
- Andersen T, Carstensen J, Hernandez-Garcia E, *et al.* 2009. Ecological thresholds and regime shifts: approaches to identification. *Trends Ecol Evol* **24**: 49–57.
- Baxter PWJ, Sabo JL, Wilcox C, *et al.* 2008. Cost-effective suppression and eradication of invasive predators. *Conserv Biol* **22**: 89–98.
- Beal B, Nault D-M, Annis H, *et al.* 2016. Comparative, large-scale field trials along the Maine coast to assess management options to enhance populations of the commercially important softshell clam, *Mya arenaria* L. *J Shellfish Res* **35**: 711–27.
- Benkwitt CE. 2015. Non-linear effects of invasive lionfish density on native coral-reef fish communities. *Biol Invasions* **17**: 1383–95.
- Chapman J, Green SJ, Solomon J, *et al.* 2019. Belize National Lionfish Management Strategy 2019–2023. Blue Ventures Conservation

- and Belize Fisheries Department. <https://bit.ly/3cLGjXQ>. Viewed 28 Sep 2020.
- Côté IM, Green SJ, and Hixon MA. 2013. Predatory fish invaders: insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biol Conserv* **164**: 50–61.
- D'Antonio C and Vitousek P. 1992. Biological invasions by exotic grasses, the grass fire cycle and global change. *Annu Rev Ecol Syst* **23**: 63–87.
- Dick JTA, Alexander ME, Riccardi A, *et al.* 2017. Functional responses can unify invasion ecology. *Biol Invasions* **19**: 1667–72.
- Dudley TL and Bean DW. 2012. Tamarisk biocontrol, endangered species risk and resolution of conflict through riparian restoration. *BioControl* **57**: 331–47.
- Elton CS. 1958. The ecology of invasions by animals and plants. London, UK: Methuen Press.
- Epanchin-Niell RS and Hastings A. 2010. Controlling established invaders: integrating economics and spread dynamics to determine optimal management. *Ecol Lett* **13**: 528–41.
- Filbee-Dexter K and Scheibling RE. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar Ecol-Prog Ser* **495**: 1–25.
- Green SJ, Akins JL, Maljković A, *et al.* 2012. Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* **7**: e32596.
- Green SJ, Dulvey NK, Brooks AML, *et al.* 2014. Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecol Appl* **24**: 1311–22.
- Gren I-M. 2008. Economics of alien invasive species management – choices of targets and policies. *Boreal Environ Res* **13**: 17–32.
- Grosholz ED. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *P Natl Acad Sci USA* **102**: 1088–91.
- Grosholz ED, Lovell S, and Besedin E. 2011. Modeling the impacts of the European green crab on commercial shellfisheries. *Ecol Appl* **21**: 915–24.
- Hadfield MG, Miller SE, and Carwile AH. 1993. The decimation of endemic Hawaiian tree snails by alien predators. *Am Zool* **33**: 610–22.
- Hansen GJA, Hein CL, Roth BM, *et al.* 2013. Food web consequences of long-term invasive crayfish control. *Can J Fish Aquat Sci* **70**: 1109–22.
- Hein CL, Vander Zander MJ, and Magnuson JJ. 2007. Intensive trapping and increased fish predation cause massive population decline of an invasive crayfish. *Freshwater Biol* **52**: 1134–46.
- Kimbrow DL, Cheng BS, and Grosholz ED. 2013. Biotic resistance in coastal environments. *Ecol Lett* **16**: 821–33.
- Kinlan BP and Gaines SD. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* **84**: 2007–20.
- Kramer AM, Dennis B, Liebhold AM, *et al.* 2009. The evidence for Allee effects. *Popul Ecol* **51**: 341–54.
- Lampert A, Hastings A, Grosholz ED, *et al.* 2014. Optimal approaches for balancing invasive species eradication and endangered species management. *Science* **344**: 1028–31.
- Laverty C, Green KD, Dick JTA, *et al.* 2017. Assessing the ecological impacts of invasive species based on their functional responses and abundances. *Biol Invasions* **19**: 1653–65.
- Letourneau DK, Armbrrecht I, Salguero Rivera B, *et al.* 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol Appl* **21**: 9–21.
- Liebhold AM, Berec L, Brockerhoff EG, *et al.* 2016. Eradication of invading insect populations: from concepts to applications. *Annu Rev Entomol* **61**: 335–52.
- Mack RN, Simberloff D, Lonsdale WM, *et al.* 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* **10**: 689–710.
- Marchi M, Jørgensen SE, Bécarea E, *et al.* 2011. Resistance and reorganization of an ecosystem in response to biological invasion: some hypotheses. *Ecol Model* **222**: 2992–3001.
- Mooney HA and Cleland EE. 2001. The evolutionary impact of invasive species. *P Natl Acad Sci USA* **98**: 5446–51.
- Myers JH, Simberloff D, Kuris AM, *et al.* 2000. Eradication revisited: dealing with exotic species. *Trends Ecol Evol* **15**: 316–20.
- Norbury GL, Pech RP, Byrom AE, *et al.* 2015. Density–impact functions for terrestrial vertebrate pests and indigenous biota: guidelines for conservation managers. *Biol Conserv* **191**: 409–20.
- Olden JD, McCarthy JM, Maxted JT, *et al.* 2006. The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (USA) over the past 130 years. *Biol Invasions* **8**: 1621–28.
- Pechar L and Mooney HA. 2009. Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* **24**: 497–504.
- Power AG. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philos T Roy Soc B* **365**: 2959–71.
- Prior KM, Adams DC, Klepzig KD, *et al.* 2018. When does invasive species removal lead to ecological recovery? Implications for management success. *Biol Invasions* **20**: 267–83.
- Sax DF and Gaines SD. 2008. Species invasions and extinction: the future of native biodiversity on islands. *P Natl Acad Sci USA* **105**: 11490–97.
- Schuster R, Wilson S, Rodewald AD, *et al.* 2019. Optimizing the conservation of migratory species over their full annual cycle. *Nat Commun* **10**: 1754.
- Simberloff D. 2001. Eradication of island invasives: practical actions and results achieved. *Trends Ecol Evol* **16**: 273–74.
- Simberloff D. 2009. We can eliminate invasions or live with them. Successful management projects. *Biol Invasions* **11**: 149–57.
- Suding KN and Hobbs RJ. 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* **24**: 271–79.
- Taylor CM and Hastings A. 2004. Finding optimal control strategies for invasive species: a density-structured model for *Spartina alterniflora*. *J Appl Ecol* **41**: 1049–57.
- Twardochleb LA, Olden JD, and Larson ER. 2013. A global meta-analysis of the ecological impacts of nonnative crayfish. *Freshwater Sci* **32**: 1367–82.
- Vander Zanden MJ, Hansen GJA, and Latzka AW. 2017. A framework for evaluating heterogeneity and landscape-level impacts of non-native aquatic species. *Ecosystems* **20**: 477–91.
- Weidel BC, Josephson DC, and Kraft CE. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. *T Am Fish Soc* **136**: 778–89.
- Wilson K, Magnuson JJ, Lodge DM, *et al.* 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and

community change in a north temperate lake. *Can J Fish Aquat Sci* **61**: 2255–66.

Witte F, Goldschmidt T, Wanink J, *et al.* 1992. The destruction of an endemic species flock – quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environ Biol Fish* **34**: 1–28.

Yamada SB. 2001. The global invader: the European green crab. Corvallis, OR: Oregon Sea Grant.

Zavaleta ES, Hobbs RJ, and Mooney HA. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol Evol* **16**: 454–59.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2277/supinfo>



A riddle, wrapped in a mystery, inside a barnacle

Approximately 80% of barnacles in Burrard Inlet, British Columbia, Canada, are infected with metacercariae, a life stage of the trematode *Maritrema gratosum*, but the origin of these infestations is unknown. Trematode parasites have a three-host life cycle and six distinct life stages. Adults usually infect shorebirds, which release the parasites' eggs in their feces; these eggs subsequently metamorphose into miracidia, which then infect snails. At this point, the miracidia develop into sporocysts that asexually produce thousands of free-swimming larvae (cercariae), which emerge from the snails. The cercariae then locate and infect the next host (a bivalve, a barnacle or other type of crustacean, or a fish) and form a metacercaria, protected by a spherical cyst, in their soft tissue (note: all three images show *M gratosum* metacercariae embedded in barnacle tissue). In the final stage of the life cycle, a shorebird eats an infected host and the metacercariae hatch into the next generation of adults.

Given the high proportion of infected barnacles in Burrard Inlet, and the density of metacercariae (typically in the hundreds) contained within them, it is a mystery as to why there are no records of snails infected with *M gratosum* at this location. Likewise, surveys at other sites of heavy barnacle infections have failed to detect substantial numbers of infected snails. One answer to this puzzle may be that the cercariae are transported over long distances by tidal currents and the infected snails (the sources of the cercariae) are relatively far away. Alternatively, these metacercariae may persist and remain viable for months or even years, such that even a relatively small number of infected snails could produce enough cercariae to infect millions of barnacles over time. Given that cercariae are known to transmit many diseases to humans (eg schistosomiasis), our barnacle mystery provides a great opportunity to study the dispersal patterns of a disease-causing agent.

Colin D MacLeod^{1,2}, Claire Armstrong¹, and Tianxin Wang¹

¹Department of Zoology, University of British Columbia, Vancouver, Canada; ²Beaty Biodiversity Museum, University of British Columbia, Vancouver, Canada
doi:10.1002/fee.2317

