Impact assessment of coastal marine range shifts to support proactive management

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Amy K. Henry[1] and Cascade J. B. Sorte[1]

[1]Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, 92697-2525 USA

Corresponding author: Cascade J. B. Sorte

phone: 949-824-6971

email: csorte@uci.edu

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Abstract

Climate change is reshuffling Earth's biota as species ranges shift to track increasing habitat temperatures. While redistribution may be necessary for species persistence, there can also be impacts on existing communities upon arrival of novel, range-shifting species. Anticipating the beneficial versus deleterious impacts of range-shifting species is essential for determining whether active management is needed, which could include employing strategies from facilitation (eg managed relocation) to suppression (eg prevention/control). We employ an impact assessment protocol developed for invasive species to evaluate potential consequences of range shifts in coastal marine ecosystems of North America. Our review demonstrates how invasion impact assessment combined with species vulnerability assessment could support decisions about management of range shifts. We found that ~50% of these shifting coastal species have had negative impacts in their expanded range. The importance of proactive management is likely to increase as the number and extent of range shifts accelerates.

In a nutshell:

- Novel species can arrive in locations due to introduction by humans or shifts in species' native ranges as habitat temperatures increase.
- There is no "one size fits all" approach to managing novel species, particularly for native range shifts: range shifts can be necessary for native species to cope with climate change, and our results show that in some cases, they lead to relatively peaceful coexistence, whereas in other cases, range-shifting species may disrupt communities.
- Our review suggests that impact assessments developed for invasive species can be used to anticipate the consequences (both negative and positive) of native species range shifts.

Introduction

Climate change is causing shifts in species' ranges in taxa and systems worldwide (Sorte *et al.* 2010, Pecl *et al.* 2017, Lenoir *et al.* 2020). As conditions become more hospitable at cold-temperature range boundaries, species can expand into areas spatially contiguous with documented native ranges. Importantly, range shifts occur piecemeal, with changes in species distributions reshuffling ecosystems. Understanding the impacts of native species range shifts is critical for anticipating effects of climate change and designing management plans for preserving biodiversity. Here, we focus on the impacts of species additions to communities at expanding range limits. We employed an impact assessment approach developed for invasive species to evaluate the consequences of native species range shifts (ie expansion of range limits) and, by so doing, explore the potential for this approach to inform management decisions.

Range shifts are both a response and driver of global change impacts: while redistribution is necessary for some species to persist, range-shifting species can have impacts in their expanded ranges that threaten current inhabitants. When climatic conditions become unsuitable, species unable to adapt in place must move or perish (Berg *et al.* 2010). Redistribution is, therefore, crucial for preventing extinctions. Across the Western Hemisphere, Lawler *et al.* (2009) predicted 10-20% (and up to 90%) species turnover in the next century based on analysis of 2,954 bird, mammal, and amphibian species. For species included in climate change vulnerability analyses (primarily terrestrial animals and plants), the proportion doomed to extinction approximately doubles in models without redistribution (Thomas *et al.* 2004, Urban 2015). Many species likely cannot shift their ranges fast enough to keep pace with climate change (Urban 2015), begging the question of whether humans should intervene on their behalf via deliberate, managed relocation (McLachlan *et al.* 2006, Hoegh-Guldberg *et al.* 2008). A main concern about managed relocation is that deliberate range shifts, as with those occurring naturally, can lead to unintended consequences.

The consequences of both range shifts and deliberate translocation of native species can include negative impacts on communities in the expanded range (ie decreases in native populations or human activities), even to the point of causing extinctions. For example, in western North America, the barred owl *Strix varia* has displaced a threatened species, the northern spotted owl *Strix occidentalis caurina* (Kelly *et al.* 2003, Long & Wolfe 2019). Barred owl removals are underway, and although eradication from its expanded range is not feasible, suppression of barred owl populations may be necessary to prevent extinction of the spotted owl (Long & Wolfe 2019). Similarly, management (via tree removal to slow spread) of the shifting southern pine beetle *Dendroctonus frontalis* appears necessary for preventing extirpation of pitch pines *Pinus rigida* in the Eastern US (Heuss *et al.* 2019). Not all range shift impacts are negative: shifting species can play beneficial roles in their expanded ranges (ie increase native populations or human activities), particularly when they increase resources. As an example, the tropical seaweed *Turbinaria ornata* provides habitat and enhances food supply for herbivorous fish in the South Pacific (Bittick *et al.* 2019), and it has chemical properties that make it potentially useful in pharmaceuticals (Ananthi *et al.* 2010). However, this seaweed also negatively impacts corals in some areas (Brown & Carpenter 2015), highlighting the importance of considering both positive and negative interactions for evaluating management options for range shifts. Given that climate change is accelerating (Cheng *et al.* 2019), there will likely be an increase in the number and rate of range shifts and the immediacy of considering whether range shifts should be actively managed. An essential step in evaluating management scenarios is range shift impact assessment (McLachlan *et al.* 2006, Hoegh-Guldberg *et al.* 2008).

Impact assessment protocols developed for invasive species could be effective tools for anticipating outcomes of native species range shifts. These assessments involve compiling published data or expert opinions to categorize species based on likely impacts. The transferability of impact assessments depends on whether a species' impacts in one (ie previously studied) location is representative of its impacts elsewhere (ie in areas where it has not yet arrived or been studied). For invasions, the impacts of a particular invasive species tend to be consistently positive or negative; however, the magnitude of these impacts can vary across locations with different environments and community members (Kulhanek *et al.* 2011, Kumschick *et al.* 2015). These caveats of using existing data from one location/community to anticipate impacts in a different location/community likely also apply to range-shift impact assessments. Impact assessments are, thus, best used to "flag species with high potential impacts" (Blackburn *et al.* 2014), and identify those that might pose high risk within groups of spreading species (eg Rockwell-Postel *et al.* 2020).

The goals and characteristics of impact assessments are the same whether novel species are invasive or native in adjacent locations: to evaluate novel species' impacts in a way that is comparable across taxa and locations and transparently incorporates the best available data with moderate effort (Blackburn *et al.* 2014, Hawkins *et al.* 2015, Eisenmenger *et al.* 2016, Turbé *et al.* 2017). At least 29 protocols exist for invasive species impact assessment, some of which identify maximum potential impacts while others predict likelihood of introduction and spread (Roy *et al.* 2017). Invasion impact assessments have yielded both species-specific information (eg prioritizing weed species for management in the northeastern US; Rockwell-Postel *et al.* 2020) as well as an understanding of the most impactful taxa and impact mechanisms (eg greater impacts of invasive mammals than birds in Europe, particularly via feeding habits; Kumschick *et al.* 2011). However, it is unclear whether impact assessments developed for invasive species will be useful for anticipating impacts of range shifts, particularly if data availability is low for native species that have not been seen as problematic or targeted for study.

The objective of this review is to assess the potential impacts of range-shifting native species on populations of interacting species in the expanded range. We applied an impact assessment modified from the Environmental Impact Classification of Alien Taxa (EICAT; Blackburn *et al.* 2014, Hawkins *et al.* 2015). The EICAT protocol was chosen because it was recently adopted for use by the IUCN (International Union for the Conservation of Nature), the body that manages the Global Invasive Species Database (www.iucngisd.org/) and Red List of Threatened Species (www.iucnredlist.org/). We also applied a modified version of the Socio-economic Impact Classification of Alien Taxa (SEICAT) protocol (Bacher *et al.* 2017), which uses the same approach and yields scores on the same scale as EICAT.

We used EICAT and SEICAT to evaluate both detrimental and beneficial impacts of range shifts in coastal marine ecosystems of North America (Table 1). We collated impacts data from both expanded and native ranges of shifting species, defining impacts based on the relationship between a range shifter's presence/abundance and the robustness of an interacting species' population or human activity. In addition to evaluating the sign and magnitude of these impacts, we tested the hypothesis that impacts increase outside of species' native ranges (as shown for many invasive species; Cure *et al.* 2012). Our study is the first to demonstrate the effectiveness of this impact assessment approach as a tool for evaluating outcomes of native species range shifts that could be incorporated into management plans.

Methods

Identification of study species

We identified 39 marine species whose poleward range limits were documented as shifting northward along the coastline (<15 km from shore) of North America, including plants, invertebrates, fish, a protist, and a bird (WebTable 1). Of these, 26 species were compiled by Sorte *et al.* (2010), and we added 13 species from an updated literature review. We searched Google Scholar (on 08/20/2019) using this search string: marine "range expansion" species "range shift". We reviewed titles and, when appropriate, text of the first 600 results, identifying 11 additional species from 14 papers (WebTable 1). We added two species from our literature files (WebTable 1).

Review of published impacts

Evidence of species' impacts was compiled from online database searches and literature review. We conducted individual Web of Science searches for the 39 shifting species using each species' scientific name (and synonyms). Papers reporting species impacts were identified by reviewing titles and abstracts. For species with >800 Web of Science results, the first 400 results were reviewed and remaining results were filtered using this search string: "ecology" OR "invas*" OR "impact". For species with <100 Web of Science results, we also performed Google Scholar searches, and relevant papers were identified from the first 400 results. Additional impact studies were added opportunistically from citations within papers found in database searches. In total, we reviewed 11,508 papers for this impact assessment of 39 range-shifting species.

Impact assessment

We evaluated environmental and socioeconomic impacts using modified versions of the Environmental Impact Classification of Alien Taxa (EICAT; Hawkins *et al.* 2015) and Socio-economic Impact Classification of Alien Taxa (SEICAT; Bacher *et al.* 2017) protocols. The EICAT and SEICAT protocols focus on impacts on native, non-human populations and human activities, respectively. Primary modifications were the inclusion of beneficial (rather than only detrimental) impacts and use of studies in species' native and expanded ranges to estimate impacts (rather than only non-native ranges). These modifications were intended to minimize the influence of study/publication bias, although we acknowledge that researchers historically focused on negative over positive interactions (Bertness & Callaway 1994) and are more likely to study/publish results of strong over weak interactions (Gurevitch & Hedges 1999).

Impacts were classified by mechanism. We identified the following mechanisms as responsible for negative impacts by shifting species on native (non-human) species:

competition, predation, herbivory, disease transmission, interaction with other invaders, physical disturbance, poisoning/toxicity, and "other" negative impacts (including those with unknown mechanisms). We also found evidence of positive ecological impacts by the following mechanisms: food provisioning, habitat provisioning, and "other" positive impacts. Our SEICAT analysis revealed socioeconomic impacts associated with alterations in health; material and immaterial assets; and social, spiritual, or cultural relations.

We assigned levels of impacts based on categories described in the EICAT and SEICAT protocols (Hawkins *et al.* 2015, Bacher *et al.* 2017). Impacts range across a semi-quantitative gradient from 1 (lowest) to 5 (highest). For each published study, we scored impacts of shifting species based on the highest level response from the categories shown in Table 1. Impact scores, thus, represent the maximum impact that has been observed. Both EICAT and SEICAT protocols were modified to incorporate positive impacts, essentially switching the direction or sign of negative impacts (Table 1). Species for which we found no published papers on impacts were categorized as "data deficient".

For both EICAT and SEICAT assessments, we collected additional information about the shifting species and study. These characteristics included taxonomic classifications, study location, and whether the study was conducted in the shifting species' "native" or non-native, "expanded" range. Ranges were defined as "native" or "expanded" based primarily on documentation within the source reporting the range shift (WebTable 1). "Expanded" ranges were designated as such conservatively, acknowledging potential lack of benchmark data for species ranges, with most range shifts documented after 1985 (Sorte *et al.* 2010). We evaluated the relationship between average EICAT impact levels in the native versus expanded range for the 7 species that were studied in both range types. This analysis was performed using a linear mixed effect model (lmer; lmerTest R package, Kunetsova 2017) in the statistical computing language R (version 4.0.2, R Core Team 2020) with range (native or expanded) as a fixed factor and species as a random effect. Visual inspection of Pearson residuals indicated no deviation from linearity or normality and no major outliers. There was also no deviation from homoscedasticity (Levene's test, $F = 0.0002$, $p > 0.05$). We validated the fit of this model against a model without random effects using AICc (nlme R package, Pinheiro *et al.* 2020).

Results & Discussion

The effectiveness of this assessment approach for anticipating impacts of range shifts depends partly on data availability, and we found that environmental impact was studied for a similar proportion of these 39 range shifters as for invasive species. Environmental impacts were documented for 32 (82%) of the 39 shifting species while 7 (18%) of the species were data deficient (WebTable 2). In reviews of invasive species impacts, the proportion of species that were data deficient ranged from 4% (2 of 50 alien mammal and bird species in Europe; Kumschick *et al.* 2011) and 18% (18 of 100 invasive plant species in the northeastern US; Rockwell-Postel *et al.* 2020) in regional studies to 71% (296 of 415 bird species; Evans *et al.* 2016) for global studies of all invasive species within a taxonomic group. Our results suggest that data availability does not preclude using assessments such as EICAT to anticipate impacts of range shifts.

Fewer data were available to assess impacts of range shifts on socioeconomic systems, for which 72% of species were unstudied and categorized as data deficient (WebTable 2). In comparison, only 26% (78 of 300) of invasive species in Europe (comprising mammals, birds, fish, insects, and plants) were data deficient for socioeconomic impacts (Kumschick *et al.* 2015). Kumschick *et al.* (2015) showed that environmental and socioeconomic impacts were highly correlated, both within and across taxonomic groups. Although this relationship supports use of an impact assessment approach, more studies of range shift impacts on human systems are needed.

In total, environmental and/or socioeconomic impacts were documented for 34 (87%) of 39 species. Our assessments were based on 184 papers, 154 papers reporting environmental impacts and 30 papers about socioeconomic impacts (~6 and ~3 papers per studied species, respectively) (Figure 1).

Published impacts of range shifts were more often negative than positive, although half (51%) of species were documented as having both beneficial and detrimental impacts across environmental and socioeconomic systems (S/EICAT score of 2+). Overall, only negative impacts were reported for 26% of species and only positive impacts were reported for 10% of species (Figures 2, 3, WebTable 2). Environmental impacts on interacting species were observed for 51% of range-shifting species. Of these, 30% were documented as having primarily positive impacts, including habitat-forming seagrass and coral, and fishery species of crab. Half (50%) of the shifting species had documented impacts that were primarily negative, most due to consumption (herbivory or predation) of native species by range-shifting gastropods and fish, as well as two shifters acting as competitors and one disease-causing protistan parasite. The remaining 20% of species had recorded impacts that were both negative and positive. These species (including sponge, coral, mangrove plant, crab, and fish species) provided food or habitat while also negatively impacting native species via consumption, competition, or physical disturbance.

The maximum impacts reported for these shifting species were Major impacts (score of 4), meaning a native species was lost or gained in a community because of the range shift, but not permanently so. In most cases, including 7 of 9 studies and 4 of 6 species, Major impacts were related to habitat availability. Creation of habitat was often beneficial but could also be detrimental. For example, habitat created by shifting mangrove species supported a native parrotfish and increased commercial fishery yields (Mumby *et al.* 2004) but also altered community structure and increased invasive species (Demopoulos & Smith 2010). Two shifting species had Major impacts via consumptive effects: the predatory sea slug *Phidiana hiltoni* decreased native sea slugs (Goddard *et al.* 2011), and *Lottia depicta*, an herbivorous gastropod (limpet), was associated with catastrophic declines in seagrass meadows (Zimmerman *et al.*

1996). We did not find evidence of global extinctions (Massive impacts; score of 5) caused by coastal marine range shifts in North America. This is perhaps not surprising given impacted species are generally characterized by high fecundity, little to no parental care, and broad dispersal capacity, which could allow population replenishment from few surviving individuals (McCauley *et al.* 2015, Le Pape *et al.* 2017). Since redistribution is likely necessary for global persistence of many species, range shifts may contribute more to biodiversity preservation than to biodiversity loss.

Most impact studies synthesized here were conducted in shifting species' native ranges, including 69% of studies on environmental impacts and 96% of studies on socioeconomic impacts. If impact assessment for range shifts only included impacts measured in species' non-native ranges, as for invasion impact assessments underway, then the number of data deficient species would increase from 13% to 63%. This pattern highlights the need for more studies in expanded ranges of shifting species as well as the importance of understanding whether impacts in the native range are indicative of impacts in the expanded range of shifting species.

We compared impacts between native and expanded ranges for 7 species that were studied in both (Figure 4, WebFigure 1). We found that species with stronger negative impacts documented in the native range were also shown to be more detrimental when shifting into new communities. However, impacts in expanded ranges tended to be more negative than impacts in native ranges, with impact increasing by more than one level between the native and expanded range (fixed effect estimate 1.78 [95% CI: 0.89, 2.59]). For 6 of 7 species, impacts were more negative in the expanded than native range, while mean impacts were the same in both ranges for 1 species (Figure 4). Species' impacts were never documented as more positive after range shifts (Figure 4). Furthermore, average impacts were negative for 4 of 7 species in native ranges and 6 of 7 species in expanded ranges (Figure 4). Thus, impacts reported in expanded ranges of shifting species were indicated by – yet often more negative than – impacts innative ranges.

Including studies from the native range not only increased the proportion of species for which impact scores could be assigned, it also led to a more balanced assessment of both detrimental and beneficial impacts of range shifts. While non-native species invasions are decreasing global biodiversity (Doherty *et al.* 2016), range shifts are becoming increasingly necessary for maintaining biodiversity (Thomas *et al.* 2004, Urban 2015) despite sometimes causing negative impacts locally (see examples above). Therefore, while a focus on negative impacts may be appropriate for invasive species management, decisions about range shifts will need to consider both negative and positive impacts. Negative impacts may be more often reported in expanded ranges where shifting species are more likely to be seen as detrimental, while positive impacts may be more often studied in native ranges where species are deemed beneficial. Therefore, while similarities between range shifts and invasions allow their impacts to be assessed using a common protocol, range shifts are unique in their potential benefits for global biodiversity. A more balanced impact assessment for range shifts, which helps to minimize the influence of study and publication bias, would ideally include positive impacts and studies conducted in native ranges.

Conclusions

Whereas managing non-native species invasions focuses on suppression (eg Hulme 2006), management of range shifts is likely to require considering a broader scope of options, including facilitation. Impact assessments developed for invasive species could be used as indicators of potential consequences of range shifts, whether they occur with or without direct human intervention. Our study of 39 range-shifting coastal marine species showed that data were available to assess environmental impacts of >80% of species, similar to the proportion of invasive species that can be assessed using the EICAT protocol. Given that this approach relies on previously published studies, and in light of likely biases in the available literature, we advocate for incorporating both negative and positive impacts studied across the native and expanded ranges of shifting species. We note that the EICAT approach is largely precautionary as it focuses on maximum recorded impacts. For well-studied species, it might be useful to consider average and most commonly reported impacts. Still, given our finding that impacts were more negative in expanded than native ranges, we should not be complacent about the potential for impacts to be more detrimental than previously recorded. Since socioeconomic impacts are rarely reported (<30% of study species), expert opinion could be solicited to fill this data gap.

Impact assessments for range shifts would ideally be paired with vulnerability assessments, both for species impacted in the expanded range and for the shifting species themselves. Both shifting species and impacted species are candidates for management, depending on their vulnerability (to changing climate or range-shift impacts), perceived value (eg to biodiversity or economy), and cost/feasibility of interventions. Managers are probably already aware of species in their jurisdiction that are endangered or of conservation concern, and impacts on these species will likely be common justification for suppressing range shifts (as with removals underway for shifting barred owls and pine beetles; Long & Wolfe 2019, Heuss *et al.* 2019). In contrast, facilitation of range shifts (and even managed relocation) might be considered when the potential range shifter is endangered. A first step in vulnerability assessment would be to determine whether the shifting species or impacted species are included on the IUCN Red List (www.iucnredlist.org/) of >32,000 species threatened with global extinction (Van der Colff *et al.* 2020). Second, for species not on the IUCN Red List, vulnerability could be assessed using an established protocol, such as the IUCN Red List extinction risk assessment protocol (eg Short *et al.* 2011). The approach proposed here, combining impact assessment with vulnerability assessment, minimizes cost because (1) both assessments rely on previously published data, and (2) by starting with the impact assessment of an identified range-shifting species, vulnerability assessments can target the shifting species itself and a subset of species in the expanded range that are likely to be impacted. Management alternatives can then be compared following a structured decision framework, such as those developed for managed relocations, which incorporate information on the risks and feasibility of options for attaining management goals (McLachlan *et al.* 2006, Hoegh-Guldberg *et al.* 2008). Even when management is not feasible, the results of these impact assessments could inform adaptation strategies (eg governance of transboundary shifts in fisheries species; Lindegren & Brander 2018, Pinsky *et al.* 2018).

The recommendations above are based on a species-specific approach to management, which may not be feasible for species that are not well studied, particularly as range shifts accelerate. Thus, future studies should seek to identify generalities in the consequences of range shifts. For example, Bradley *et al.* (2019) demonstrated that for invasions, impacts accrue more rapidly from species of higher trophic levels, highlighting the need for more proactive management of invasive predators and herbivores. As with invasive species, impacts of range shifts are likely to be greatest for species with highest population sizes and individual effects. Therefore, strong impacts of range shifts might be indicated by characteristics such as life history strategies and trophic levels of shifting species or community-level resistance to disturbance in expanded ranges (Catford *et al.* 2009, Wallingford *et al.* 2020). However, generalizing impacts between species groups is premature, as our study revealed high variability between species, with strong impacts by species at both the top and bottom (eg habitat-forming primary producers) of the food chain and few taxonomic patterns (WebTable 2).

Our findings serve as evidence that there is no “one size fits all” approach for managing range shifts, which depend on the level and type of impacts combined with human interests and options for intervention. Of range shifts reviewed here, ~50% led to observed negative impacts on environmental and/or socioeconomic systems (Figures 2,3). At the same time, redistribution is increasingly important for global persistence of these species, some of which have already experienced contractions of low-latitude range boundaries (eg Fenberg *et al.* 2014, Timbs *et al.* 2019). While our review focused on impacts of species addition (through range shifts or managed relocation), this approach could also be used to illuminate impacts of species loss in areas of range contraction. In summary, impact assessments developed for invasive species combined with vulnerability assessments is a promising approach for evaluating whether range shifts are, on balance, detrimental or beneficial. The next step in proactive management involves determining the level of negative impacts that we are willing to accept, particularly given beneficial impacts and extinction risks for range-shifting species.

Data Availability

The final dataset is available on Dryad, DOI 10.7280/D1770W.

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Figure captions

Figure 1. Number of published studies on environmental and socioeconomic impacts of 39 coastal marine species that have undergone range shifts in North America.

Figure 2. Maximum negative (red) and positive (blue) scores for environmental impacts of range-shifting species based on the EICAT protocol (Table 1).

Figure 3. Maximum negative (red) and positive (blue) scores for socioeconomic impacts of range-shifting species based on the SEICAT protocol (Table 1).

Figure 4. (a) Comparison of impact scores averaged across studies conducted in native versus expanded ranges. Values range from -4 (major detrimental impact) to +4 (major beneficial impact) for 8 species. The quadrants represent possible scenarios. For quadrants lying along the diagonal 1:1 line, direction of impacts is the same in both ranges (negative at bottom left, positive at top right). Alternately, impacts could switch from negative to positive (top left) or from positive to negative (bottom right) during the range shift. Species in this analysis included (b) black mangrove *Avicennia germinans*, (c) mangrove snapper *Lutjanus griseus*, and (d) dark unicorn whelk *Mexacanthina lugubris*. Photo credits: (b) AR Hughes, (c) SA Bedgood, (d) DJ Eernisse.

Table

Table 1. Risk assessment impact levels

Impact Level		EICAT (Environmental impacts)		SEICAT (Socioeconomic impacts)	
		Negative	Positive	Negative	Positive
1	Minimal	Impacts possible (based on known interactions) but no change in native fitness observed	Impacts possible (based on known interactions) but no change in native fitness observed	Impacts possible (based on known uses) but no change in human activities observed	Impacts possible (based on known uses) but no change in human activities observed
2	Minor	Decreased fitness of a native species	Increased fitness of a native species	People continued to participate in an activity but with difficulty	People began to participate in an activity but with difficulty
3	Moderate	Decreased population size of a native species	Increased population size of a native species	Fewer people participated in an activity	More people participated in an activity
4	Major	Extirpation of a native population that could reestablish if the expander were removed	Establishment of a native population which would be lost if the expander were removed	An activity was suspended locally but would continue if the expander were removed	An activity commenced locally but would stop if the expander were removed
5	Massive	Extirpation of a native population which would not recover even if the expander were removed	Establishment of a native population which would persist even if the expander were removed	An activity was permanently lost in a location	An activity was permanently adopted in a location

Figure 1

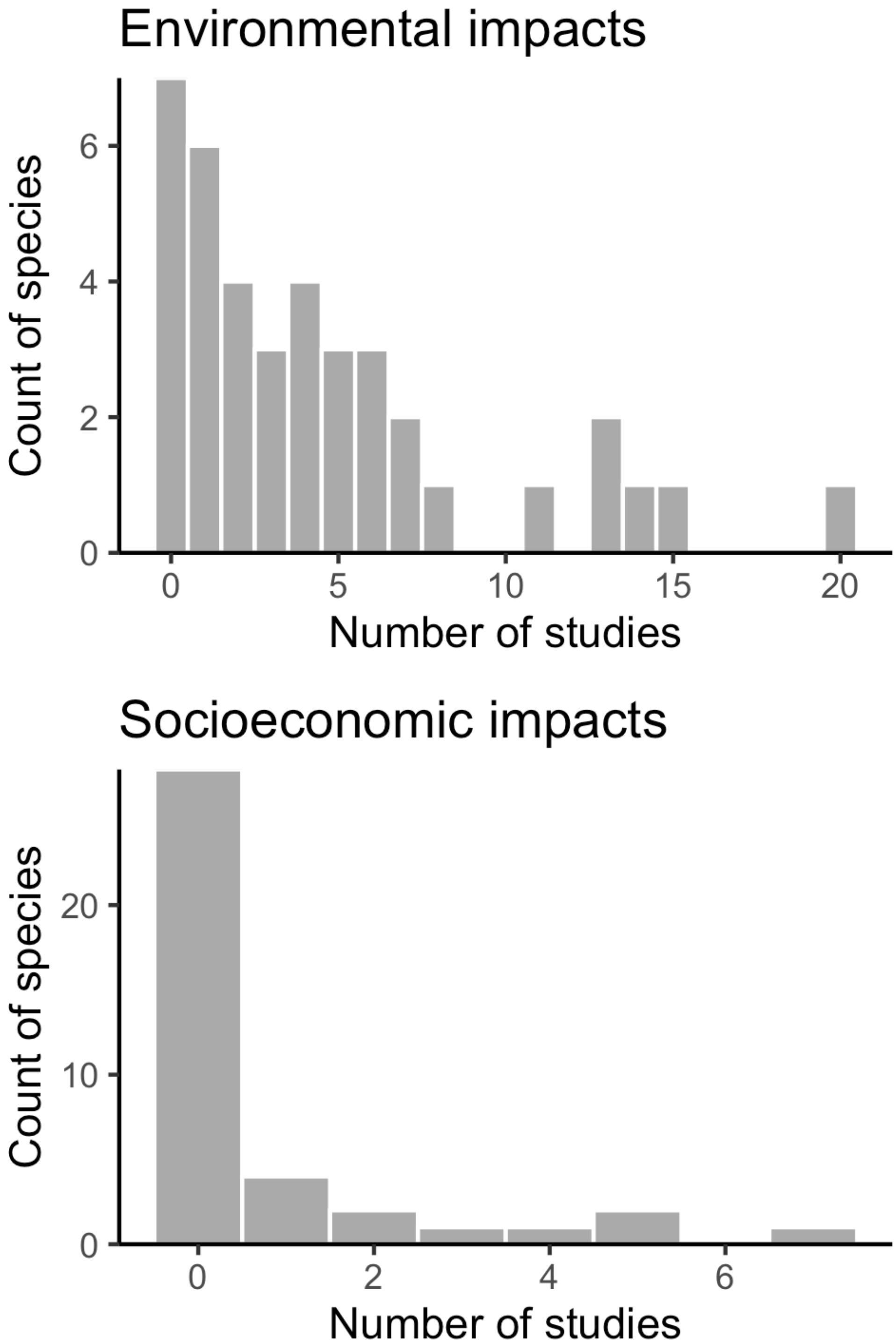
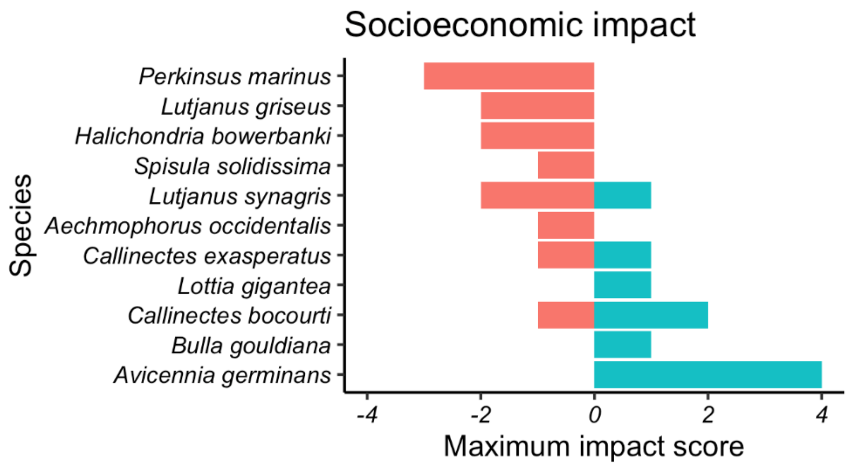

Environmental impacts
Count of species
0
2
4
6
0
5
10
15
20
Number of studies
Socioeconomic impacts
Count of species
0
10
20
0
2
4
6
Number of studies

Figure 2


Environmental impact
Phidiana hiltoni
Lottia depicta
Perkinsus marinus
Nicholsina usta
Hermosilla azurea
Norrisia norrisi
Mexacanthina lugubris
Caprella scaura
Acanthinucella spirata
Lottia gigantea
Lacuna unifasciata
Kelletia kelletti
Glossaulax reclusiana
Avicennia germinans
Urophycis regia
Thysanoessa inspinata
Spisula solidissima
Rhizophora mangle
Petrolisthes armatus
Bulla gouldiana
Brachidontes adamsianus
Aratus pisonii
Tetraclita rubescens
Pseudochama exogyra
Halophila johnsonii
Acropora cervicornis
Lutjanus synagris
Lutjanus griseus
Halichondria bowerbanki
Aechmophorus occidentalis
Acropora palmata
Halophila decipiens
Species
-4
-2
0
2
4
Maximum impact score

Figure 3



Socioeconomic impact
Perkinsus marinus
Lutjanus griseus
Halichondria bowerbanki
Spisula solidissima
Lutjanus synagris
Aechmophorus occidentalis
Callinectes exasperatus
Lottia gigantea
Callinectes bocourti
Bulla gouldiana
Avicennia germinans
Species
-4
-2
0
2
4
Maximum impact score

Figure 4a

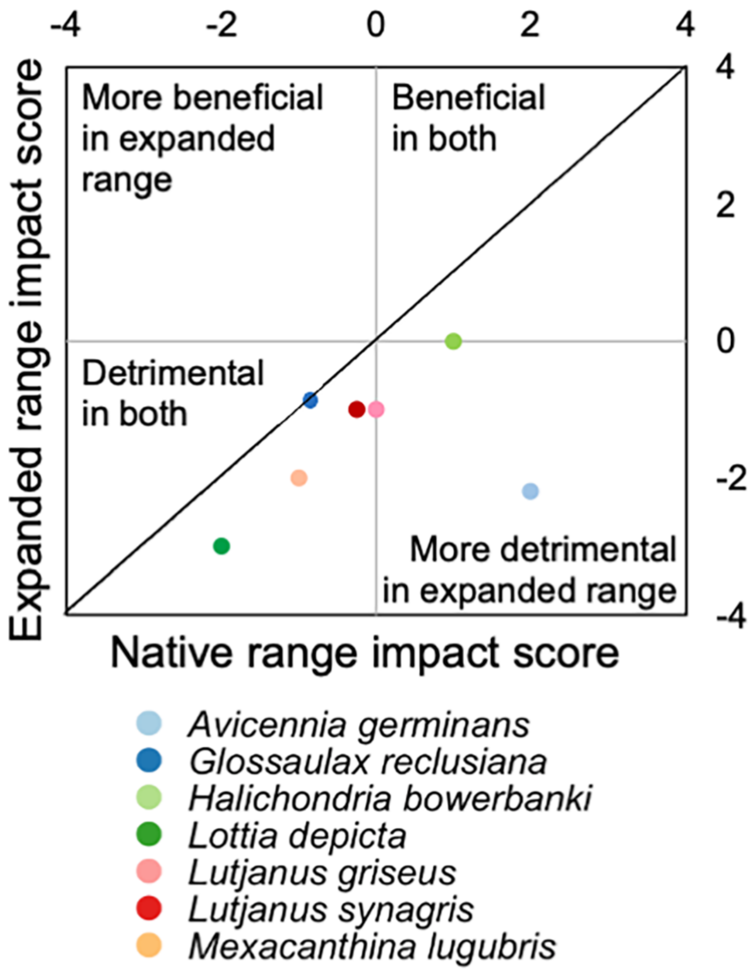

-4
-2
0
2
4
More beneficial in expanded range
Beneficial in both
Detrimental in both
More detrimental in expanded range
4
2
0
-2
-4
Expanded range impact score
Native range impact score
Avicennia germinans
Glossaulax reclusiana
Halichondria bowerbanki
Lottia depicta
Lutjanus griseus
Lutjanus synagris
Mexacanthina lugubris

Figure 4b

Figure 4c

Figure 4d