Selecting species for restoration in foundational assemblages

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Abstract

1. Humans have long sought to restore species but little attention has been directed at how best to do so for rich assemblages of foundation species that support ecosystems, like rainforests and coral reefs that are increasingly threatened by environmental change.
2. We developed a two-part triage process for selecting optimized sets of species for restoration. We demonstrated this process using phenotypic traits and ecological characteristics for reef building corals found along the east coast of Australia. Without clear linkages between phenotypic traits and ecosystem functions, the first part of the triage hedges against function loss by ensuring an even spread of life history traits. The second part hedges against future species losses by weighting species based on characteristics that are known to increase their ecological persistence to current environmental pressures—abundance, species range and thermal bleaching tolerance—as well as their amenability to restoration methods.
3. We identified sets of ecologically persistent and restorable species most likely to protect against functional loss by examining marginal returns in occupancy of phenotypic trait space per restored species.
4. We also compared sets of species with those from the southern-most accretional reef as well as a coral restoration program to demonstrate how trait space occupancy is likely to protect against local loss of ecosystem function.
5. *Synthesis and applications*. A quantitative approach to selecting sets of foundational species for restoration can inform decisions about ecosystem protection to guide and optimize future restoration efforts. The approach addresses the need to insure against unpredictable losses of ecosystem functions by investing in a wide range of phenotypes. Furthermore, the flexibility of the approach enables the functional goals of restoration to vary depending on environmental context, stakeholder values, and the spatial and temporal scales at which meaningful impacts can be achieved.

Keywords

Restoration; foundation species; triage; phenotypic traits; ecosystem function; hermatypic corals

Introduction

The rate and extent of environmental change experienced by contemporary ecosystems have resulted in major deviations from their historical state (Hobbs et al., 2011). Conservation alone may therefore no longer suffice to preserve biodiversity and ecosystem functions, and restoration is often considered a now required addition. The objective of ecosystem restoration is, through human intervention, to recover a disturbed or degraded ecosystem as far as possible towards some previous state. Interventions in the coastal and marine realm can be direct, such as propagation and field deployment of habitat builders through seeds (e.g., seagrass in Virginia – Orth et al., 2020), propagules (e.g., oysters in South Australia - Vanderklift et al., 2020), early recruits (e.g., kelp - Fredriksen et al., 2020; coral - Randall et al., 2020) or parts of adult tissues (e.g., coral gardening - Rinkevich 2014). Indirect interventions, such as physical stabilization of degraded reef structures are also possible (Ceccarelli et al., 2020).

To date, the augmentation or reintroduction of one or few species has been the most common approach, such as the restoration of the endangered Caribbean coral species *Acropora cervicornis* and *A. palmata* (Ladd et al., 2019), the reintroduction of the greater bilby in some parts of Australia (Lott et al., 2020), the gray wolf across parts of Europe and North America (Ripple et al 2014), and assisted colonization of the Tasmanian Devil to the Australian mainland (Brainard 2020). However, climate change is now affecting many assemblages of foundation species in most if not all the world's ecosystems—forests, kelp forest, and coral reefs—leading to a necessary broadening of focus of restoration activities to encompass more species and their contributions to ecosystem functioning (Brudvig & Mabry 2008; Ladouceur & Shackelford 2021).

Prioritizing sets of species for the restoration of biodiverse ecosystems is a challenging task, and different approaches for decision making have been used. For instance, some approaches focus on the roles that species play in providing particular ecosystem goods or services, including carbon storage in rainforests (Strassburg et al., 2020) or mangrove forests (Adame et al., 2014), or reef accretion on coral reefs for coastal protection (Bellwood et al., 2019). Another often used focus is on keystone species: species that maintain the organization, stability, and function of their communities, and have disproportionately large, inimitable impacts on their ecosystems (Hale et al., 2018). Alternatively, weedy pioneer species may quickly restore habitat functions such as such as providing shelter or stabilizing substratum, such as the emphasis on fast growing acroporids in coral gardening initiatives (Bostrom-Einarsson et al., 2020). However, the objective selection of species based on defined ecological, functional and logistical criteria are rare (Suding et al., 2004; Lamb 2018). Some examples exist for forest restoration (Meli et al., 2013), and some have used linkages between phenotypic traits and ecosystem functions to select species (Giannini et al., 2017; Rayome et al., 2019).

An overarching challenge is that restoration initiatives need to anticipate future ecosystem states which are expected to be very different due to the escalating impacts of climate change (Rogers et al., 2015; Gaitán□Espitia & Hobday 2021). Faced with complex ecosystems, multiple threats to biodiversity and limited funding, conservation practitioners must prioritize investment into different management options, including restoration actions, and difficult decisions must be made about which sets of species to allocate resources to (Game et al., 2018). Strategic decisions must be taken about supporting those most likely to do better to improve future persistence and resilience, and those that will struggle and potentially push them through a period of elevated and prolonged stress; especially those that are already closer to their existing physiological limits, like reef-building corals. Protecting habitat-forming species such as corals is imperative for securing the ecological functions and socio-economic services they provide such as reef building, habitat and food provisioning for commercially important species, primary production, nutrient recycling, natural products, and social, cultural and recreational opportunities.

In this paper, we developed a two-part triage process for selecting sets of species for the restoration or maintenance of foundational assemblages, for which we use reef-building corals as an example. The first part centered on the restoration of ecosystem functions provided by foundational assemblages, such as habitat engineering (Ellison et al., 2005) (Fig. 1). However, rather than targeting specific ecosystem functions (Fig. 1a), we propose to minimize loss of function by maximizing phenotypic variation (Fig. 1b) for several reasons. First, mechanistic linkages between phenotypic traits of species and functions are poorly understood, especially for coral reefs (Bellwood et al., 2019). Second, the species that support specific functions are likely to differ depending on the situation (e.g., disturbance history) and site-specific conditions. Third, maximizing life history variation minimizes the risk of wholesale species loss, because no species is at a selective optimum in all situations and environments (Stearns 1992). Fourth, important ecosystem functions, such as habitat engineering and ecological succession, tend to be supported by a broad range of life history combinations (e.g., builders, fillers and cementers [Goreau 1963]; weedy, competitive and stress-tolerant [Darling et al., 2012]). Finally, a bet hedging approach also acts to increase phylogenetic diversity because many life history traits are evolutionarily conserved (Westoby et al., 2002).

The second part of the triage process is to select species based on characteristics that make them better equipped to avoid depletion and resist or recover from large-scale events like fires or marine heatwaves (Fig. 1c). For example, species with small range sizes and small local populations generally have a higher extinction risk (Staude et al., 2020), while species with higher local abundances tend to bounce back faster following disturbance (Halford et al., 2004). Often there are synergistic relationships—for example, extinction risk tends to be greater for geographically limited and locally rare species (double jeopardy; Brown 1984)—but not always (Hughes et al., 2014). Meanwhile, some species are more tolerant to disturbances and gradual changes that are expected to become more frequent or more intense in the future through rapid adaptation. Suitability of species to restoration can also be considered as a characteristic of ecological persistence; albeit one requiring human intervention (Suggett et al., 2019). For example, restoration may be facilitated by the use of species that can be easily propagated in the laboratory via sexual reproduction, grown in nurseries and outplanted, or manipulated in the field (Rinkevich 2020; Randall et al., 2020). Furthermore, some phenotypic traits and ecological characteristics make some species better candidates for restoration than others. For instance, it is easier to generate coral fragments from branching species than from massive species, therefore most restoration efforts on coral reefs have historically focused on branching corals (Bostrom-Einarsson et al., 2020). Similarly, restoring local areas with species that have large geographical ranges will improve connectivity (Hock et al., 2017).

The overall aim was to develop a quantitative approach to select a set of *n* species for restoration, recognizing that the goals of restoration can vary enormously across systems. The approach we developed aims to maximize the probability of maintaining phylogenetic diversity and ecosystem function, and therefore protect against a range of sensitivities to future stressors. We demonstrate this approach with reef building corals found on the east coast of Australia, including the Great Barrier Reef, a region that has declined severely over the past few decades (De'ath et al., 2012; Hughes et al., 2017). Here, coral reef restoration activities are already underway to address the local-scale depletion of coral populations (Boström-Einarsson et al., 2020; Howlett et al., in review) and larger scale restoration interventions are in the research and development phase (Anthony et al. 2020). Although the data and results are only illustrative at this stage, and further scrutiny is required before making formal restoration decisions at appropriate and manageable scales (McAfee et al., 2021), it provides a quantitative, reproducible and adaptable basis for selecting species for restoration projects and restoration research.

Materials and methods

Spectrum of life histories—The first part of the process required collation of quantitative phenotypic traits for species that capture as many life history trade-offs as possible (Gallagher et al., 2020), such as acquisition-conservation and propagule size-number (Westoby et al., 2002). For our demonstration, we use a dataset for 396 species found along the east coast of Australia from McWilliam et al. (2018) with the following traits: growth rate, corallite width, rugosity/branch spacing, surface area per unit volume, colony height, maximum colony size/diameter, and skeletal density. The trait data enabled us to capture important dimensions of species life history, ranging from fast to slow growth (Darling et al., 2012), fragile to robust morphologies (Zawada et al., 2019), and small to large colonies that drives up colony fecundity (Alvarez-Noriega et al., 2016). The trait space was calculated using a principal components analysis (PCA) of the seven traits and is presented in Fig. 2a for the 396 species.

We also viewed the trait space through the lens of one ecosystem function, reef building, by adopting Goreau's (1963) classification of reef species into builders, fillers and cementers; an approach that has been supported by modern synthesis (González-Barrios & Alverez Filip 2018). Within the McWilliam et al. (2018) trait space, builders were classified as species with the highest values of size, height, and volume; fillers with largest values of size and rugosity; and cementers with the largest sizes and smallest height values (Fig. 2a, red vectors). Ecosystem functions such as reef building and habitat construction requires a broad range of life histories—ranging from slow growing, potentially large builders (i.e., late successional species) to dense skeleton, encrusting cementers to fast growing, morphological complex fillers (i.e., weedy or early successional species). Other functions tend to require specific trait combinations (Fig. 2b). For example, coral species with higher surface area to volume ratios, rugosities and growth rates tend to generate habitat complexity that is reportedly important as fish habitats (Graham & Nash 2013) and have a high value for human uses, such as tourism and recreation, because they are generally considered aesthetically appealing (Marshall et al., 2019).

While there are many definitions of phenotypic trait diversity (Villéger et al., 2008), our goal under a hedging strategy was to evenly capture the largest area of trait space with the fewest species, and therefore to ensure a spread of species along important trait dimensions. This goal was accomplished by iteratively removing the species closest to other species in the two-dimensional area defined by PC1 and PC2 (which captured about 70% total trait variation) until a given number of species *n* remained. Selection could also happen at higher dimensions to capture higher levels of variation. We tried two approaches to measure the proximity of species using R (R Core Team 2021): (1) the areas of Voronoi cells using the *voronoi.mosaic* function in the *tripack* package (Renka et al., 2020), and (2) the nearest neighbor distances using the *nndist* function in the *spatstat* package and only considering the single closest species (i.e., k=1; Baddeley et al., 2015). Proximity values were normalized at each iteration by dividing by the maximum distance or area, depending on the approach. A grid-based approach was used to assess trait diversity throughout the study, whereby a grid of a given resolution was superimposed onto the trait space (e.g., a 5 by 5 cell grid is shown in Fig. 3a and a 10 by 10 cell grid in Fig. S2). Trait diversity was the proportion of possible grid cells with at least one species; redundancy was the mean number of species in occupied possible grid cells.

Ecological persistence—For the second part of the triage process we focused on three characteristics (ecological abundance, geographic range size and thermal bleaching susceptibility) broadly defined as factors contributing to ecological persistence of reef building coral species. We acknowledge that these characteristics will depend on current taxonomic designations that are currently being revised (Cowman et al., 2020). We used typical abundance of species data from Veron (2000) and geographic distribution data from Hughes et al. (2013) downloaded for the 396 species from the Coral Trait Database (Madin et al., 2016). Ecological abundance was categorized by Veron (2000) as common, uncommon and rare, which we normalized as 1, 0.5 and 0.25, respectively. Geographic extent was normalized by dividing the range size of each species by the maximum range size for a species. Normalizing puts characteristics on the same scale (i.e., between 0 and 1) (Fig. S1). Weightings can also be applied to characteristics of ecological persistence to augment or diminish their importance, but we did not do so here.

Thermal bleaching susceptibility is an increasingly relevant characteristic for coral ecological persistence, but it is context dependent, highly variable, and poorly understood. Nonetheless, we use the Coral Bleaching Index (BI) from Swain et al. (2016) to demonstrate how this variable might be included in the triage analysis. BI is a value between 0 and 100, where higher values correspond with more thermally vulnerable species. Therefore, we normalized BI by dividing by 100 and subtracting the result from 1 (i.e., species with values closer to 1 are more resistant to bleaching based on Swain et al. [2016]). BI values were available at the species level for 212 of the species, and therefore genus level BIs were used for the remainder of the analysis in order to retain all 396 species.

Restoration of reef corals is a relatively new field (Hein et al., 2021), and so there is little long-term knowledge of what makes species more or less amenable to the restoration process. A meta-analysis of coral restoration studies ranked the use of coral growth forms in restoration projects (Boström-Einarsson et al., 2020). While this ranking likely reflects a historical focus on coral gardening (i.e., fragmentation) as well as specific situations, such as the demise of branching *Acropora* species in the Caribbean, we nonetheless utilize this ranking as an index of species amenability to restoration. Species growth form was downloaded from the Coral Trait Database and species were ranked from 1 to 6: columnar (1), tabular (2), encrusting (3), foliose (4), massive (5), and branching (6), which includes corymbose and digitate. This ranking was normalized by dividing values by six.

Pairwise associations between PC1, PC2 and normalized ecological persistence variables for species are shown in Fig. S1. Weighting species by characteristics was done by multiplying normalized values. Species with values closer to 1—i.e., large ranges, common, and resistant to bleaching—were considered ecologically persistent. To redirect focus of species selection to vulnerable species, normalized variables were subtracted from 1 before proceeding. For example, we also explored the triage process for species that were wide ranging and common, but susceptible to bleaching.

Triage assessment—We compared triage results with two contrasting reef assemblages. The first was the southern-most accretional reef assemblage along the east coast of Australia, Lord Howe Island, built by approximately 50 coral species; however, we only include the 15 most common species for our analysis, having greater than 5% mean cover (Table S1). Contrasts were made by comparing trait combinations in the Lord Howe assemblage with those generated by the triage process with the same numbers of species (n=15). The second set of species are those used for out-planting for fragments by the Coral Nurture Program on the Great Barrier Reef throughout the first two years of its planting activity across six northern GBR high value tourism reef sites (~20,000 out-plants; August 2018 - April 2020; Howlett et al., in review). The program is run by tourism operators, and so tends to focus on abundant, fast growing branching species with recognised aesthetic values to the tourism industry. Contrasts were made by comparing trait combinations of the 39 Coral Nurture Program species with those generated by the triage process for n=39 species.

Results

The nearest neighbor distance method produced the most even spread of species in the trait space (Fig. 2c, points) because the Voronoi area method could not calculate areas for peripheral points (Fig. 2c, crosses) that were inadvertently retained during the iterative species removal process.

Selecting species based solely on maximizing species spread in trait space (i.e., via nearest neighbor distances) resulted in levels of occupancy in the trait space that were significantly greater than random (Fig. 3a, yellow line sitting largely above the shaded 95% confidence band).

Conversely, selecting species based solely on ecological persistence led to both the lowest occupancy in the trait space (i.e., spread of morphological and life history traits) and the highest levels of redundancy (Figs. 3a and 3b green curves, respectively). These levels of occupancy and redundancy were not significantly different to randomized species selection (black curves in Figs. 3a and 3b, respectively, where the green "persistence" curves are captured by the shaded 95% confidence bands). Selecting species based on both ecological persistence and trait diversity resulted in some loss of trait diversity, but with levels of occupancy much greater than ecological persistence alone (Fig. 3, red curves). Marginal returns in terms of occupancy per species was high (approximately 5% per species) for the combined triage scenario (i.e., red curve, Fig. 3a) up until n=11 species, medium (approximately 2% per species) between from n=11 to n=28, and low (<0.3% per species) above n=28. The general patterns shown in Fig. 3 were robust to the cell size of the grid used to calculate occupancy (Fig. S2); with the proviso that more species are required to maintain specified levels of occupancy and redundancy for finer grids. For example, the region of medium marginal returns occurred between n=29 and n=55 for the 10 by 10 cell grid (Fig. S2A, red curve).

Based on marginal returns, the optimal number of species selected occurred somewhere between 11 and 28. Fig. 4 shows triage values when selecting n=20 species at different stages of the process for two scenarios: (1) considering ecologically persistent species (large geographic range, ecologically abundant and resistant to bleaching) (Fig. 4a) and (2) considering large geographic ranges and ecologically abundant species that are susceptible to bleaching (Fig. 4b). While there is some overlap among the triage stages, Fig. 4 demonstrated how focal species can change throughout the selection process. It also shows the selection outcomes of switching species that are better ecologically, but are difficult to restore based on our criteria, while simultaneously retaining an even spread of species in the trait space. Fig. 2d contrasts triage for 20 species with and without consideration of trait diversity, illustrating that, while cementers are captured either way, because they tend to be ecologically persistent species, while builders and fillers are not captured to the same extent if focused solely on ecological persistence characteristics.

The 15 species of Lord Howe Island assemblage showed lower trait diversity and higher redundancy than would be produced by the triage process (Fig. 3, asterisks). Nonetheless, these species occupied three highly distinctive trait combinations that largely overlap with the three functional groups originally put forward by Goreau (1963) (Fig. 2e). The 39 species of the Coral Nurture Program showed trait diversity markedly lower than expected by randomly selecting species (Fig. 3a), resulting in high levels of redundancy (Fig. 3b). Indeed, the Lord Howe Island assemblage showed similar levels of occupancy as the Coral Nurture Program with less than half the species (Fig. 3a). Fig. 2f illustrates that these out-planted species are the fast growing, high surface area to volume ratio species, with the exception of *Galaxea fascicularis* (Fig. 3e, red arrow); they also only tend to capture Goreau's filler species category.

Discussion

The triage process developed here identified coral species for restoration projects based on both ecologically beneficial characteristics and diversity of life history trait values. Selection based on ecological persistence is important for hedging against future species loss, while phenotypic trait diversity is important for hedging against both species loss and local ecosystem function loss. The importance of individual species in ecosystem functions are poorly understood, particularly for reef corals, and therefore our tactic was to prioritize an even spread of species across the trait space rather than prioritizing particular phenotypic trait values or targeting regions in the trait space (e.g., Fig. 2b). Even spread across the trait space (measured as gridded occupancy) increased with the number of species selected; however, marginal returns declined at relatively low numbers of species (~20 species, Fig. 3a). However, this depended on the resolution at which the trait space was gridded (Fig. S2). How finely spread species should be across trait space for preserving particular ecosystem functions remains an open question. Meanwhile, the number of species that can be selected for a restoration project will ultimately depend upon project goals, as well as resource and logistical constraints. The flexible triage process developed here can serve as a framework for such decisions.

The species lists shown in Fig. 4 is an illustration of outputs that include one potential planning process, hence the anonymous labelling, as they are based on a relatively narrow set of ecological characteristic and phenotypic trait data. Future studies may build on our initial analyses by including a broad range of traits (rather than primarily morphological traits presented here) and imputing trait values for species with missing trait data (Fig. 1). For instance, certain *Acropora* species are underrepresented in Fig. 4a due to their high bleaching sensitivity. We used the colony growth form ranking by Bostrom-Einarsson et al. (2020) as the suitability for restoration trait. This trait is relevant for coral gardening approaches that fragment, grow and then out-plant adult colonies (Rinkevich 2014). However, for prioritization of species in restoration initiatives based on propagation of sexually produced coral stock (dela Cruz and Harrison 2020), we recommend traits other than growth form to be used for defining species' suitability for restoration, such as the mode of reproduction (large amounts of sexually produced offspring are easier to obtain from broadcast spawning as compared to brooding species; Doropoulos et al., 2019), high early life survivorship, and fecundity (species with higher fecundity can provide larger numbers of sexually produced offspring; Alvarez-Noriega et al., 2016). An obstacle for selecting species for restoration based on sexual reproduction is that the knowledge of husbandry is limited for many spawning coral species, and it will always be challenging to obtain high abundances of sexually produced offspring from brooding species (Randall et al., 2020). However, the triage process can be used to highlight where husbandry effort should be directed. For example, Fig. 4 contrasts the best set of species for restoration based on ecological persistence and trait diversity (middle columns in panels a and b); however, this list changes when also considering which of these species are amenable to fragmentation and gardening approaches (last columns). Ideally, coral husbandry and out-planting research should focus on reducing this mismatch (e.g., Baria□Rodriguez et al., 2019).

Our understanding of the species and traits that drive reef functions and services is still emerging, placing severe limitations on our capacity to select foundation species for restoration. Many reviews have dealt with the importance of ecosystem functions and services on coral reefs (Harborne et al., 2006, Brandl et al., 2019; Woodhead et al., 2019), including in the context for reef restoration practices (Hein et al., 2021). However, for corals, the experimental and observational evidence linking species to functions is still limited (Brandl et al., 2019), perhaps because of the long timescales of reef-building. For example, recent restoration work from the Florida Keys achieved large increases in the cover of *Acropora cervicornis* but little benefit to broader ecological functions (Ladd et al., 2019). Furthermore, in their blueprint for protecting coral reef functions, Bellwood et al (2019) suggest a hierarchical approach, recognizing that all functions are not equal, and that priority functions are likely to be context specific and should be defined in specific restoration objectives. Selecting species based on functions is therefore likely to vary across systems depending on the specific environment, and the values of the local stakeholders. Our triage approach addresses both these limitations by hedging against loss of range of function by capturing a wide range of morphological and life history traits, while simultaneously enhancing the probability that these traits persist in a range of environments. Given the uncertainty inherent to all restoration efforts, we suggest that better knowledge of functions and a clear vision of the goals of restoration is likely to enhance rather than supersede this triage approach.

Restoration efforts should explicitly consider the capacity of species to persist in future environments. An increasingly visible pattern is that there are species that are likely to persist in future predicted environments ('winners') and those that are likely to decline in future environments ('losers') (Adam et al., 2021). Whether to protect the hardy or the vulnerable is a widespread debate throughout conservation biology. For example, when selecting protected areas, the decision to protect areas of imminent threat or resistant areas generating the best returns is highly context-dependent (Sacre et al., 2019). Similarly, whether to select winners or losers for restoration is likely to depend on the severity of the threat to the ecosystem, and the traits and functions that are most critical to ecological integrity. Indeed, a species-oriented focus on restoration is likely to favor rare or depleted species with low persistence, while ecosystem-based restoration is likely to favor foundation species that are dominant and therefore drive ecosystem functions. The triage approach developed here is specifically designed so that both these viewpoints can be incorporated.

This paper's goal was to develop and present a simple and flexible process for decision making around target species for restoration using real and interpolated data. However, the data and results presented here should not be used for decisions without further consideration, consultation and analysis. For example, a multi-criteria decision-making approach is one pathway (Gouezo et al., 2021). Expert elicitation by coral reef scientists is needed but inadequate, and this process should also include other stakeholders (managers, tourism operators) and pivotally, First Nations people. Moreover, the value of restoration as a management intervention per se must be evaluated against or complement alternative tools, such as protected areas, fish aggregation devices, and artificial structures, and the outcomes of such assessments vary from one ecosystem function to another (Rogers et al 2015). The ultimate goals of restoration, and particularly the ecosystem functions being targeted, should be based on the scale at which restoration has the greatest impact. Moreover, the success of coral restoration hinges upon addressing local and global actions that facilitate natural coral growth and reproduction, such as regulating climate, overharvesting and land-use.

Authors contributions

All authors conceived the idea during a working group meeting organized by MJHvO and KQ. JSM and MM developed the idea, gathered data and ran analyses. JSM, MM, KQ and MJHvO wrote the first draft. All authors critically revised drafts and added intellectual content.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

All data and code are available at https://github.com/jmadinlab/species_choice

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Figure 1. Selecting sets of species for restoration with a two-part triage approach. The orange panel shows ecological functions that are important or threatened. If mechanistic linkages between life history traits and functions are established, then triage could focus on specific high-priority functions (left blue panel). Alternatively, a bet hedging approach that maximizes the diversity of functional and life history traits increases the likelihood that multiple functions are performed across a range of environments (right blue panel). Next, the species supporting functions are narrowed down further to include only those with characteristics that enhance or diminish their chances of persisting (green panel), resulting in different lists of species (yellow panel).

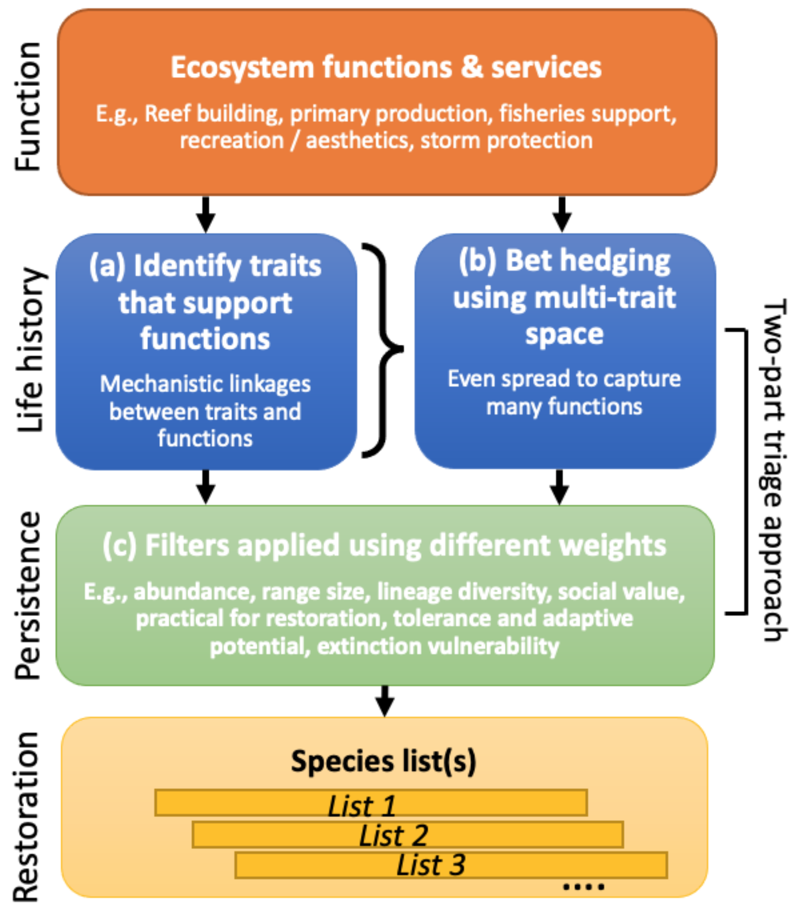
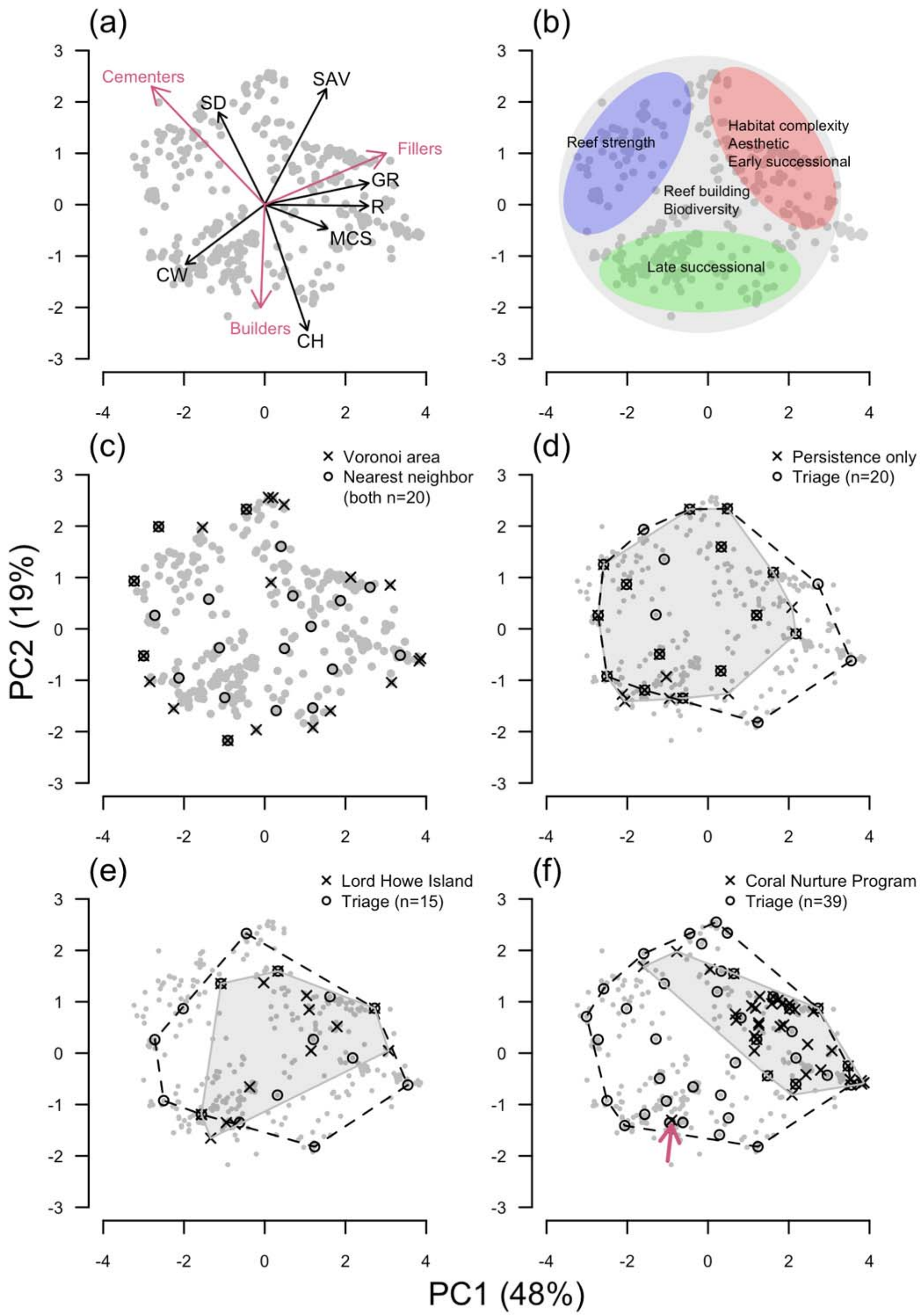


Figure 2. Phenotypic trait space is represented as the first two principal component axes for 396 east coast Australia coral species. (**a**) The trait loadings: growth rate (GR), corallite width (CW), rugosity/branch spacing (R), surface area per unit volume (SAV), colony height (CH), maximum colony size/diameter (MCS), and skeletal density (SD). Red vectors are Goreau's (1963) categories of essential reef builders. (**b**) An overlay illustrating where several functions approximately lie in trait space. Some functions require species broadly across the space, whereas others only a limited region of the space. (**c**) Selections of evenly spread species (n=20) calculated using nearest neighbor distances (points) and Voronoi cell areas (crosses and dashed line). (**d**) Selections based on ecological persistence characteristics only (crosses and grey shading) and then with the addition of trait diversity weighting (points) demonstrating the two-part triage. (**e**) The 15 common Lord Howe Island species (crosses) and 15 species selected using the triage approach (points). (**f**) The 39 Coral Nurture Program species (crosses) and 39 species selected using the triage approach (points). The red arrow shows an outlier species, *Galaxea fascicularis*.


(a)
Cementers
SD
SAV
Fillers
GR
R
MCS
CW
Builders
CH
(b)
Reef strength
Habitat complexity
Aesthetic
Early successional
Reef building
Biodiversity
Late successional
(c)
× Voronoi area
o Nearest neighbor
(both n=20)
(d)
× Persistence only
o Triage (n=20)
(e)
× Lord Howe Island
o Triage (n=15)
(f)
× Coral Nurture Program
o Triage (n=39)
PC2 (19%)
PC1 (48%)

645

Figure 3. (**a**) Proportion occupancy and (**b**) redundancy in trait space as a function of number of species n using a 5 by 5 cell grid (inset in panel **a**). Regions of high, medium and low marginal returns delineated with dotted vertical lines. Included are symbols that show trait diversity and redundancy for common species at Lord Howe Island (*n*=15) and for the Coral Nurture Program (*n*=39). The grey shaded region shows 95% CIs for randomized species selection.

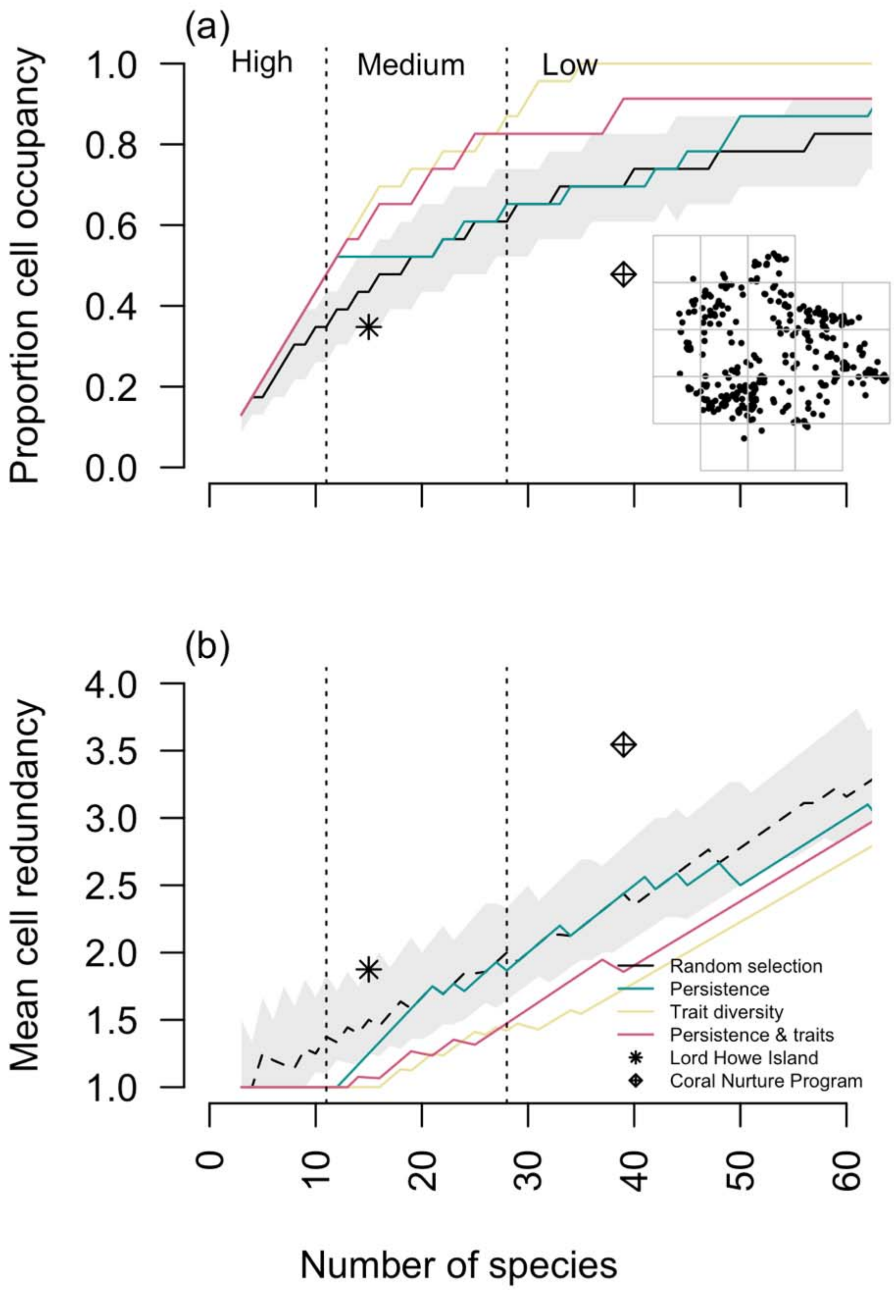
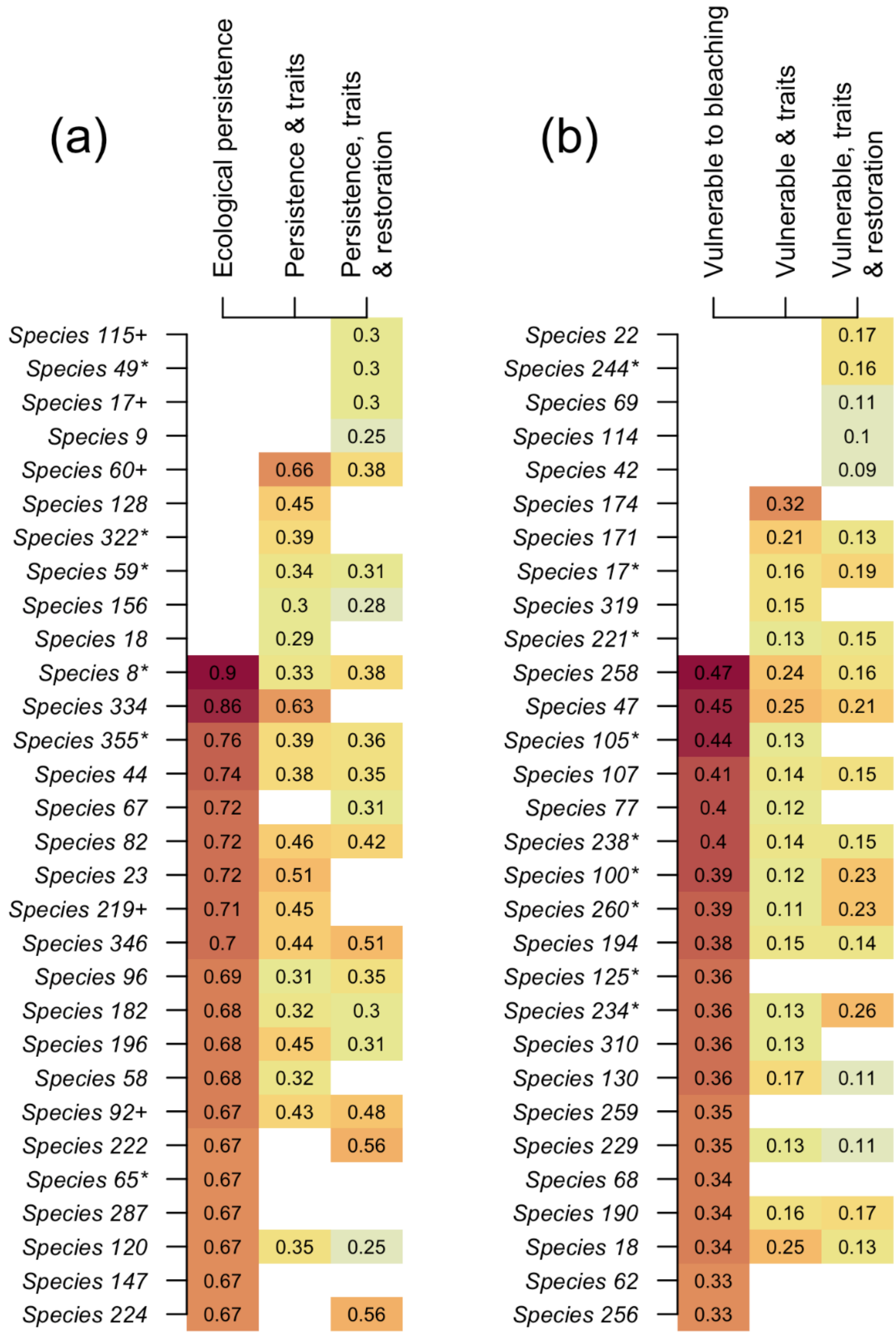


Figure 4. Species selected (n=20) at different stages of the triage process when focusing on (**a**) ecological persistent species in terms of range size and local abundance, bleaching resistance, and suitability for restoration, and (**b**) species that have a large range size and are ecologically abundant, vulnerable to bleaching, and suitable for restoration. Values (and heat colors) correspond with a species triage score at successive stages. Asterisks (*) denote species found at Lord Howe Island; pluses (+) denote Coral Nurture Program species from Howlett et al. (in review).


(a)
Ecological persistence
Persistence & traits
Persistence, traits & restoration
Species 115+ 0.3
Species 49* 0.3
Species 17+ 0.3
Species 9 0.25
Species 60+ 0.66 0.38
Species 128 0.45
Species 322* 0.39
Species 59* 0.34 0.31
Species 156 0.3 0.28
Species 18 0.29
Species 8* 0.9 0.33 0.38
Species 334 0.86 0.63
Species 355* 0.76 0.39 0.36
Species 44 0.74 0.38 0.35
Species 67 0.72 0.31
Species 82 0.72 0.46 0.42
Species 23 0.72 0.51
Species 219+ 0.71 0.45
Species 346 0.7 0.44 0.51
Species 96 0.69 0.31 0.35
Species 182 0.68 0.32 0.3
Species 196 0.68 0.45 0.31
Species 58 0.68 0.32
Species 92+ 0.67 0.43 0.48
Species 222 0.67 0.56
Species 65* 0.67
Species 287 0.67
Species 120 0.67 0.35 0.25
Species 147 0.67
Species 224 0.67 0.56
(b)
Vulnerable to bleaching
Vulnerable & traits
Vulnerable, traits & restoration
Species 22 0.17
Species 244* 0.16
Species 69 0.11
Species 114 0.1
Species 42 0.09
Species 174 0.32
Species 171 0.21 0.13
Species 17* 0.16 0.19
Species 319 0.15
Species 221* 0.13 0.15
Species 258 0.47 0.24 0.16
Species 47 0.45 0.25 0.21
Species 105* 0.44 0.13
Species 107 0.41 0.14 0.15
Species 77 0.4 0.12
Species 238* 0.4 0.14 0.15
Species 100* 0.39 0.12 0.23
Species 260* 0.39 0.11 0.23
Species 194 0.38 0.15 0.14
Species 125* 0.36
Species 234* 0.36 0.13 0.26
Species 310 0.36 0.13
Species 130 0.36 0.17 0.11
Species 259 0.35
Species 229 0.35 0.13 0.11
Species 68 0.34
Species 190 0.34 0.16 0.17
Species 18 0.34 0.25 0.13
Species 62 0.33
Species 256 0.33