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PRACTITIONER'S PERSPECTIVE

Using plant functional traits to restore Hawaiian rainforest

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Introduction

Ecosystem restoration efforts are carried out by a variety of individuals and organizations with an equally varied set of goals, priorities, resources and time-scales. Once restoration of a degraded landscape or community is recognized as necessary, choosing which species to include in a restoration programme can be a difficult and value-laden process (Fry, Power & Manning 2013; Jones 2013). Species choice in restoration is often carried out with limited ecological information, particularly in regard to species interactions, successional processes and resource-use patterns. Selecting species can be particularly problematic in systems where there is no available baseline data on historical communities, or when restoration to a historic state is not feasible for ecological, logistic or economic reasons. In such cases, it may be preferable to focus on restoring site 'functionality' rather than returning to a historic baseline composition. We present a method for species selection in restoration, based on the collection of plant functional trait data. Using this method, managers can develop species mixtures with desired properties, including expected predictions of interspecific interactions and potential changes in biotic and abiotic conditions.

To illustrate this approach, we present a case study in Hawaiian lowland wet forests (HLWF) in which plant species for a restoration project were chosen based on their functional traits, in order to help land managers achieve their restoration goals while at the same time allowing researchers to better understand invasion resistance and ecosystem functioning. In our case, our choices led to the development of hybrid ecosystems including both native and introduced species. However, the approach that we present is not limited to novel or hybrid ecosystem creation, because the candidate species examined and functional traits measured are determined by the user.

Whereas restoration usually implies a return to historic conditions, there is also growing attention to what some authors have called 'intervention ecology' (*sensu* Hobbs *et al*. 2011). This view emphasizes maintaining ecosystem services and functions (Hobbs *et al*. 2011). The contrast between these frameworks has been widely debated in the literature, and we do not intend to advocate the merit of one view over the other here. Rather, we present the logic behind a functional trait approach, describe why its use is feasible in a Hawaiian lowland forest and present a step-by-step approach to the method that can be applied to a wide variety of ecological systems. While we readily acknowledge that in our study system, we cannot return to a pre-human state, we still consider our approach 'restoration' in a broad sense.

How do we perform functional restoration?

Functional trait theory holds that characteristics or traits of each species reflect their resource use and life-history trade-offs (Reich 2014). A body of evidence shows that plant traits vary continuously, in predictable ways, along resource availability gradients – suggesting that species' functional traits can be linked to ecosystem properties and to ecosystem services (Lavorel 2013). Many studies have suggested that a robust image of a species' functional profile can be obtained by considering traits related to resource acquisition (e.g. foliar nitrogen, leaf area), resource limitation (e.g. midday leaf water potential, $\delta^{13}C$-integrated water-use efficiency, leaf mass per area), reproductive investment (e.g. height, seed mass, dispersal type) and resource allocation patterns (e.g. leaf mass per area, specific root length, wood density) (Drenovsky & James 2010; Douma *et al*. 2012; Sonnier *et al*. 2012; Fry, Power & Manning 2013). For restoration, selecting species with certain functional trait values can influence species interactions (including competition) and ecosystem properties (Suding *et al*. 2008). For example, if creating a more

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fire-tolerant community is necessary, practitioners could select species that increase fine-fuel loads or species whose presence will favour succession from forest to grassland. Other considerations relevant to managers include importance to local wildlife, ability to serve as nurse logs, nitrogen-fixing properties, etc.

Restoration in a Hawaiian context – testing ideas in a model system

The Hawaiian archipelago offers a unique setting for testing novel approaches to applied ecological questions. On one hand, Hawai'i is considered a model system for ecological research because of the combination of well-defined biotic and abiotic gradients with extreme examples of adaptive radiation (Vitousek 2004). On the other hand, like many isolated oceanic islands, the Hawaiian Islands have been extremely vulnerable to invasion and anthropogenic disturbance. The combination of simplicity and susceptibility presents a distinctive platform for conservation research.

Hawaiian lowland wet forests in particular present serious challenges for restoration and conservation. This forest type only exists as remnant patches, is always populated by invasive plant and animal species, and occurs near human habitation, where non-native propagule pressure is likely to be high (Zimmerman *et al.* 2008). In such ecosystems, it is important to recognize that not all non-native species are equally problematic. For example, many Polynesian introductions in Hawai'i have persisted in the landscape for up to 1000 years without becoming invasive. In addition to being culturally important, many non-invasive, non-native species have functional trait values, which are not present in the native flora. Breadfruit and coconut are two species that fit both of these criteria: they are not classified as invasive, and they have large leaves and seeds, unlike most native plants. From a restoration perspective, we aimed to test the hypothesis that designing communities with greater diversity of functional trait expression will lead to more invasion-resistant communities (Funk *et al.* 2008; Drenovsky & James 2010). To do so, we examined the functional traits of species using multivariate analysis; the technique projects each species to a specific x,y location in 'trait space,' which should reflect that species' functional profile.

Our restoration experiment was carried out at the Keaukaha Military Reservation (KMR) within the municipality of Hilo. This site retains a HLWF, which has a canopy that contains significant numbers of native tree species; however, it also has a long history of disturbance, and invasive trees represent up to half of the basal area (Ostertag *et al.* 2009). A previous removal experiment in this forest has shown that removal of invasive species alone is not enough to get a native forest back, despite its positive influence on seedling recruitment of native species (Cordell *et al.* 2009; Ostertag *et al.* 2009). Given current conditions, the forest is poised to lose most of its native species and become like most of the forest patches remaining in the lowlands – almost exclusively non-native dominated.

The trait-based method we used employs five steps. We illustrate the method's use in HLWF; however, it need not include the use of non-native species, and it is exportable to other ecosystems.

STEP 1. ARTICULATE OBJECTIVES AND CONSTRAINTS

Land managers at KMR are charged with specific targets developed by the US military. These are as follows: (i) conserving and encouraging the regeneration of native biodiversity at the site, (ii) controlling invasive species and (iii) encouraging carbon storage on the landscape. Because restoring this area to an all-native ecosystem is no longer economically feasible, we elected to create hybrid ecosystems. Our experimental communities were assembled using species whose combined functional trait profiles addressed these three management goals to meet restoration objectives of the main stakeholders.

STEP 2. SELECT APPROPRIATE FUNCTIONAL TRAITS

We had two main considerations for choosing the traits on which to base our species selection. First, we wanted to estimate the 'functional role' or 'strategy' (*sensu* Reich 2014) of different species within HLWF environments, and secondly, we wanted to identify specific traits that would address our restoration objectives. We first looked at the overall distribution of HLWF species in trait space and then focused on how different species expressed particular traits that were relevant to our restoration objectives.

The functional traits measured (Table 1) were derived from literature and field data. We included traits that are informative in the ecological context of HLWF. For example, knowing that light (rather than nutrient or water availability) is the primary limiting resource for native species in this forest (Ostertag *et al.* 2009), we included a suite of traits related to light capture (as well as canopy and understorey architecture; including leaf : petiole ratio, plant height and canopy shape). Many of the traits we measured are informative of more than one aspect of a plant species' ecological strategy, and some traits can be used as proxies for others, which are more difficult to measure. For example, we included both maximum plant height and seed mass as proxies for dispersal distance (see Thomson *et al.* 2011).

STEP 3. DETERMINE POOL OF SPECIES FOR TRAIT SAMPLING AND RESTORATION POTENTIAL

The potential species pool included native species thought to have been present at the site historically, native species currently found at the site and non-native species already

Table 1. List of functional traits measured in 25 Hawaiian lowland wet forest sites

Functional trait	Biological significance	Trait range	Source of data
Leaf : petiole ratio	Light acquisition and self-shading	2·81–200·00	Measured
Leaf thickness	Resource acquisition, longevity and resource use	0·17–1·40	Measured
Leaf mass per area (LMA)	Photosynthesis, resource availability and longevity	8·24–469·22	Measured
Foliar nitrogen (%)	Concentration of RuBisCO, photosynthesis and fast-to-slow strategies	0·55–2·25	Measured
Foliar carbon (%)	Leaf construction and resource use	32·62–49·63	Measured
Foliar carbon : nitrogen	Leaf longevity and fast-to-slow strategies	14·82–79·78	Measured
Foliar phosphorus (%)	Leaf quality	Trace–0·30	Measured
Stem specific gravity (g cm^{-3})	Diameter growth rate, mortality rate, hydraulic capacity and carbon storage	0·16–1·51	Measured
Water-use efficiency	Water-use efficiency, resource use and acquisition	42·26–154·16	Calculated
Max plant height (m)	Competitive vigour, plant fecundity and light acquisition	5–30	Bibliographic
Seed mass (g)	Dispersal, longevity and survival	<0·01–2·50	Bibliographic
Stature*	Dispersal, longevity and carbon storage	1–3	Observation
Canopy architecture†	Light interception and stability	1–3	Observation
Leaf area (cm^2)	Photosynthetic capacity and resource allocation	2·8–>1000	Measured
Water content (%)	Resource use and allocation, and fast-to-slow strategies	2·59–85·9	Measured

*Vertical position in the forest (1 = understorey, 2 = mid-storey, 3 = overstorey).
†Clustering of branches relative to the canopy (1 = bottom, 2 = middle, 3 = top).

found in the region that are believed to pose low invasion risk. To address the latter, we based our decisions on the Hawaiian Weed Risk Assessment score (Daehler *et al.* 2004; see http://www.botany.hawaii.edu/faculty/daehler/wra/). In a past study at KMR, woody species richness was nine native species and 10 introduced species (Zimmerman *et al.* 2008).

Due to a lack of formal records of species occurrence and poor pollen preservation, it is difficult to ascertain which species would have been found historically in any given area of HLWF. Because we suspect that some native species once found at KMR have been locally extirpated, we cast a wide net in order to determine which species could potentially be used for restoring the forest. We included native species with similar environmental requirements that could have occurred in HLWF, based on historical range descriptions by Wagner, Herbst & Sohmer (1999) and previous field experience.

Once the list of potential species was compiled (including 17 non-native and 19 native species), we eliminated species which were too difficult to sample or propagate, and species for which sufficient data were not available – reducing our pool to 16 native species and 15 non-native species. Other limiting factors that practitioners should consider include economics (e.g. cost of seeds, plants, labour or time), logistics (e.g. availability of species, project or budget timelines), resilience to climatic change or disturbance regimes, as well as the goals and expectations of stakeholders.

STEP 4. COLLECTION AND PREPARATION OF TRAIT DATA

We sampled plant traits across the full range of conditions in which HLWF is found regionally in order to account for both site and environmental heterogeneity. In total, we sampled traits at 25 sites throughout east Hawai'i Island, in addition to using existing data from the literature. By far, the most time-consuming and effort-consuming steps in making species choices by using traits are creating the potential species pool and collecting trait data. However, compilations of trait data are increasingly common world-wide. A variety of data sets are available either directly from researchers and agencies involved in the region (e.g. the Australian Virtual Herbarium) or from collaborative data base compilations (e.g. TRY (http://www.try-db.org), DRYAD (http://datadryad.org/) or LEDA (http://www.leda-traitbase.org/LEDAportal/).

Once the trait data were assembled, we grouped the information for each trait into quartiles in order to account for both analytical constraints and the nature of trait data. Because we considered both multiple traits and multiple species, making meaningful comparisons was often challenging. For example, measures of seed mass spanned many orders of magnitude from <0·001 to 576 g, while the maximum difference in leaf thickness measured no more than 0·4 mm (Table 1). Furthermore, sometimes it is necessary to compare ratios and categories to numerical data. The use of quartiles places more importance on the relative differences in trait values. This approach emphasizes species which are 'outliers' rather than species that display the 'middle range' (i.e. the most or least effective water use vs. the species whose values are nearest to the group mean). This type of data manipulation is appropriate to the multivariate ordination analysis we later employ.

STEP 5. DATA ANALYSIS AND FINAL SPECIES CHOICE

We used a principal components analysis (PCA) to show how the selected species are arranged, relative to one another, in trait space and to provide an idea of each spe-

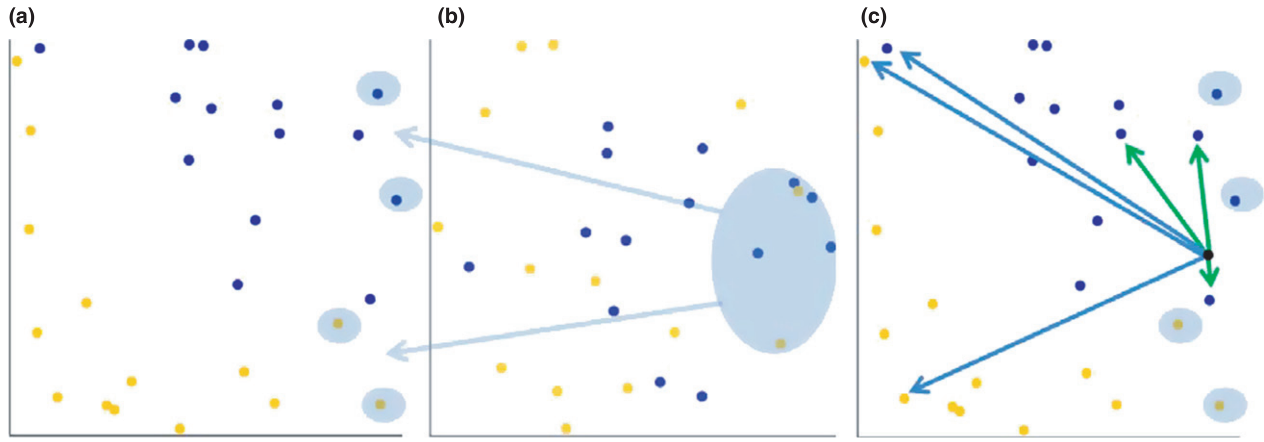

Fig. 1. Overview of the ordination process used to select species. (a) Principal component analysis (PCA) showing all species: natives in blue and non-natives in yellow. Species circled are the 'core species' identified in the second PCA as being 'high-carbon species'. (b) PCA highlighting carbon-related traits; the species circled are the ones selected for having the slowest carbon turnover, according to their position in the PCA. (c) On the main PCA, once a centroid has been found (centre point between the four core species), species are identified as having redundant (similar – geometrically closest on axis 1) or complementary (less similar – geometrically distant on axis 1) trait profiles.

cies' functional profile. Other multivariate techniques could be substituted. An important outcome of the PCA was the prominent separation of native and non-native species in distinct areas of the graph, primarily based on leaf mass per area, carbon : nitrogen ratio and foliar nitrogen (Fig. 1a). This result reinforces that species in Hawai'i with different biogeographic origins are functionally divergent. Hawaiian species tend to be conservative in regard to growth and nutrient acquisition, whereas the non-native species tend towards faster life-history strategies.

Carbon turnover rates are substantially higher in invasive-dominated communities than they are in native plant communities (Hughes *et al.* 2014). With this in mind, we ran an additional PCA using only traits associated with carbon cycling (including specific gravity, foliar chemistry and maximum plant height) to find which species from our pool have the greatest likelihood of slow rates of carbon turnover (Fig. 1b). We identified two groups of four 'core species' whose trait profiles indicate either slow or moderate carbon turnover, and then located these core species on the first (general) PCA of all species traits (Fig. 1a). Based on Euclidian distances within the general PCA, we determined a centroid point equidistant from all four species in each group and then selected groups of additional species that were closer (i.e. most similar and potentially most redundant) and furthest (i.e. least similar and potentially most complementary) to each centroid (Fig. 1c). The motivation for this selection was that we are trying to determine whether combinations of species whose traits are more dissimilar (complementary) or similar (redundant) confer greater invasion resistance in the hybrid forests (Funk *et al.* 2008).

Once species are displayed in trait space, a variety of decisions can be made based on their relative functional profiles. While our process included two PCAs, for some restoration objectives, decisions could be made with only one (Fig. 1a). In our case, pragmatic and logistical concerns were addressed at this point. For example, one of our species was removed, because although it was culturally important, and functionally a good fit, it is unable to maintain itself without direct, ongoing human intervention. Alternatively, when several species proved to be functionally similar, final species choice was based on pragmatic considerations such as seedling cost, availability within given time frames or projected time to maturity. In short, the process allows for an unbiased way to let the data dictate a first step, and then, the practical concerns of practitioners can be layered onto the final species choices.

Conclusions

To date, multiple studies have evaluated the role of functional traits in ecosystems and/or been carried out in controlled settings and relatively simple ecosystems such as grasslands (Drenovsky & James 2010; Fry, Power & Manning 2013; Lavorel 2013). We show that a trait-based approach can also be used in a tropical forest system. Because the metrics are based on site-specific restoration objectives, this approach is generalizable, flexible and transferable across ecosystems and taxa. Once refined, the approach can be applied with relatively little effort by managers.

We named our project Liko Nā Pilina, which translates loosely to 'the budding new relationships', to emphasize the developing associations among the species, and the intertwining of fundamental science questions and the practical needs of land managers faced with a formidable task made more daunting by lack of information on how to achieve their restoration goals. While it is too early to determine if the treatments met our objectives, results

1 year after planting show >90% survival of outplants and increased seedling recruitment by native species. By creating hybrid ecosystems using both native and non-native species (many of which are culturally significant), the project melds together traditional and contemporary approaches to forest management. This has proved attractive to the general public, school groups and summer programmes, allowing us to tap into an eager set of volunteers. In our experience, the level of community engagement is unusual for science-based restoration experiments. Thus, this new type of restoration can fulfil many goals, providing a rigorous way to choose species for restoration as well as providing a simple framework that is appealing to local communities.

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Data accessibility

Data have not been archived because this article does not contain data.

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Biosketch

Rebecca Ostertag is interested in understanding and conserving the functioning of tropical ecosystems. Her work in both Latin America and Hawai'i includes studies of nutrient accumulation and cycling, as well as long-term forest dynamics. **Laura Warman** has spent time working in rainforests in Australia, New Zealand, Mexico and Costa Rica. Laura's work oscillates between blue-sky plant ecology and more applied ecology and conservation. She hates leeches. **Susan Cordell** has a long-standing interest in the intersection between ecology and restoration, especially in dryland systems. Her work focuses on ecophysiology, invasion biology and the role of fire in Hawaiian dry ecosystems. **Peter M. Vitousek's** work has focused on nutrient cycling in tropical and temperate forests, particularly the cycling and regulation of nitrogen and phosphorus. In his work, he has also evaluated ecosystem consequences of biological invasion by exotic species.