Full length article

Linking plant and animal functional diversity with an experimental community restoration in a Hawaiian lowland wet forest

Rebecca Ostertag [a,*], Esther Sebastián-González [b], Robert Peck [c], Trebor Hall [a], Jihoo Kim [d], Nicole DiManno [a], Donald Rayome [e], Susan Cordell [f], Paul Banko [g], Amanda Uowolo [f]

[a] Department of Biology, University of Hawai'i at Hilo, USA
[b] Departamento de Biología Aplicada, Universidad Miguel Hernández, Elche, Spain
[c] Hawai'i Cooperative Studies Unit, University of Hawai'i at Hilo, Pacific Island Ecosystems Research Center, Hawaii National Park, HI, USA
[d] School of Integrative Biology, University of Illinois, Urbana-Champaign, IL, USA
[e] US Army Pacific, Pohakuloa Training Area, Hilo, HI, USA
[f] Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI, USA
[g] U.S. Geological Survey, Pacific Island Ecosystems Research Center, Hawaii National Park, HI, USA

ARTICLE INFO

ABSTRACT

Testing how plant restoration influences animal taxonomic and functional diversity can shift restoration projects beyond mainly plant community considerations. We incorporated multi-trophic interactions into restoration by describing an ongoing functional trait-based restoration experiment in Hawaiian lowland tropical wet forest (Liko Nā Pilina Experiment), where litter arthropods are examined from a functional perspective thereby linking plants and higher trophic levels. We hypothesized that (1) communities with greater plant functional trait diversity would have cascading effects through food webs, increasing animal diversity and network complexity, and (2) increases in animal species and network complexity would be stronger for restoration efforts in plant communities with more complementary functional traits than those with more redundant traits. We examined experimental treatments of planted communities with the same species richness but with different plant functional trait profiles based on (1) rates of expected carbon turnover (slow or moderate), and (2) the similarity of their functional trait measurements (redundant or complementary), as determined by functional dispersion calculations. Initial data on arthropod communities and leaf litter decomposition rates revealed linkages between plant functional traits and arthropod community diversity. Overall, we argue that a more comprehensive evaluation of restoration accounts for both functional diversity and the multi-trophic nature of animal and plant communities. Developing restoration projects based on plant functional traits that influence both plant and invertebrate species provides a new paradigm, and the incorporation of both native and non-native (but non-invasive) plants shows promise in restoring ecosystem function in disturbed lowland tropical forests.

© 2020 Elsevier Inc. All rights reserved.

1. Introduction—the value of incorporating multi-trophic interactions into restoration planning

Traditionally, restoration ecologists have assumed that "if you build it, they will come," and thus have focused on manipulating plant community structure. However, a recent call is to shift restoration planning toward considerations beyond the plant community (Fraser et al., 2015), encouraging testing basic hypotheses of how plant restoration influences animal species and their functions. Wright et al. (2009) argue for a biodiversity and ecosystem function approach to restoration, in which there is some aspect of waiting for species to colonize on their own along with planned species additions. This paper highlights the value of incorporating multi-trophic interactions into restoration planning for two major reasons. First, plant diversity is important in creating species-rich animal communities (Scherber et al., 2010; Rzanny and Voigt, 2012). Also, restored systems are often less complex than natural systems, at least in the early stages of development, and therefore it can be easier to examine multi-trophic interactions in restored areas, allowing for new insights and experimental tests that could be better controlled than in natural systems (Vander Zanden et al., 2006).

The literature relating biodiversity and ecosystem function suggests two potential mechanisms for promoting functional ecosystems. The **diversity hypothesis** proposes that with greater species diversity (in the general sense), there are greater opportunities for complementary use of resources (niche complementarity), and ultimately greater ecosystem productivity and stability (Tilman et al., 2006; Allan et al., 2011; Craven et al., 2016). Experimental approaches designed to examine

the relationship between diversity and productivity have been varied but generally have been restricted to primary producers (Schuldt et al., 2019). Alternatively, the **mass ratio hypothesis** (Grime, 1998) predicts that it may not be total plant species diversity, but rather the dominant biomass contributors that most influence ecosystem-level processes such as productivity and nutrient cycling. Several empirical studies support this hypothesis (Garnier et al., 2004; Díaz et al., 2007; Fortunel et al., 2009; Laughlin, 2011), but again these experiments have focused mainly on the plant community.

Empirical studies identifying interactions among different trophic levels (e.g., Qian, 2007; Hertzog et al., 2016) suggest two conclusions: (1) changes in plant diversity affect higher trophic levels, where diverse plant communities lead to species-rich animal communities (e.g., Haddad et al., 2001), and (2) the effect of plant diversity is not the same for all the trophic levels and is generally strongest for herbivores (Scherber et al., 2010; Schuldt et al., 2011). However, theoretical studies suggest that the increase in animal species diversity through the trophic pyramid may be more related to differences in plant functional diversity than to plant species richness per se (Cardinale et al., 2011; Devoto et al., 2012). While functional diversity can have many different meanings, in this paper it is based on what organisms do in terms of their interactions with other species and with the abiotic components of the environment (Petchey and Gaston, 2006). From a practical sense, functional diversity often refers to a suite of measurements that quantify a species role in the ecosystem, based on the set of functional traits chosen to be measured. Functional diversity represents the suite of these metrics and can include functional richness, functional evenness, functional divergence, and functional dispersion (Villéger et al., 2008). To date, there are only a few studies that have used the approach of linking functional diversity to multi-trophic interactions (Schittko et al., 2014; Deraison et al., 2015; Lefcheck and Duffy, 2015; Kuppler et al., 2016; Schuldt et al., 2019), yet they can reveal how interactions among species will vary by ecosystem type and across trophic levels (Schuldt et al., 2019). Also, multi-trophic interaction studies are lacking in restoration projects (Fraser et al., 2015).

The diversity of plant communities may affect not only animal species diversity (Junker et al., 2013), but also the way species interact with each other (i.e., the interaction networks) among different trophic levels (Haddad et al., 2009). Plant species diversity is known to affect the structure of the interaction networks linking plants with herbivores, carnivores, and detritivores (Rzanny and Voigt, 2012; Junker et al., 2013), and functional diversity may have similar effects. Changes in the organization of the interactions may have important consequences for ecosystem functioning (Montoya et al., 2006; Thébault and Fontaine, 2010). For example, using simulations, several studies have identified that some non-random organizations of the interactions among species lead to more stable and robust communities (e.g., nestedness in plant-animal mutualistic interactions, Rohr et al., 2014). However, besides the increasing literature on the relationship between species diversity and interaction structure (Rzanny and Voigt, 2012; Junker et al., 2013), very little is known about the multi-trophic changes in the structure of the interactions driven by plant functional diversity (but see Kuppler et al., 2016).

2. Plant functional diversity—the first step to consider in restoration design

Species choice is one of the most difficult decisions involved in the restoration process (Rayome et al., 2019). When the plant species to be used in restoration can be chosen deliberately (see Ostertag et al., 2015), the concept of plant functional diversity can be incorporated, encompassing metrics that focus on the magnitude, variation, and dissimilarity in species' functional traits (Schleuter et al., 2010). Considering functional diversity rather than species diversity may be a more promising approach to address questions of how species influence the structure and function of ecosystems (Laureto et al., 2015), community assembly (Bhaskar et al., 2014), and restoration (Fig. 1).

Several studies support that increases in animal species diversity may be related to differences in plant functional diversity (Fig. 1). For example, Gillison et al. (2013) found that plant functional diversity was the best predictor of termite diversity in Sumatra. Likewise, Dinnage et al. (2012) identified that plant phylogenetic diversity (which is highly related to functional diversity) strongly predicted the diversity of arthropods at higher trophic levels and suggested that phylogenetically distant species occupy different functional roles in the community. High plant functional trait diversity may also promote functionally diverse animal communities as niche opportunities expand in the higher trophic levels (Fig. 1). For example, Chillo et al. (2017) found that after a human disturbance the functional diversity values of both animal and plant community decreased, while ŠipoŠ et al. (2017) found a similar trend in the functional diversity metrics between vascular plants and spiders after canopy thinning. However, this link between plant and animal functional diversity is not universal (Spake et al., 2016) and the number of studies addressing the cascading effects of functional diversity at different trophic levels is still small.

3. Case study—incorporation of plant functional diversity into food web restoration

The application of functional trait theory in restoration and management is an exciting new approach that can be used to understand the persistence of species and ecosystems and to build model communities with desired ecosystem functions. We have an ongoing functional trait-based restoration experiment in a lowland tropical wet forest in Hawai'i. Only a small fragmented portion of Hawaiian lowland wet forest remains due to agricultural clearing and development. The remaining habitat is heavily invaded by non-native plants and animals, and previous attempts to maintain these forests as all-native species assemblages was unsustainable in terms of labor, logistics, and cost (Ostertag et al., 2009; Cordell et al., 2016).

The **Liko Nā Pilina Experiment** located in Hilo, Hawai'i (19°42.15N, 155°2.40W) selected species with a broad range of functional traits (i.e., high functional divergence) (Ostertag et al., 2015; Rayome et al., 2018). The experiment was designed to examine how different combinations of functional traits planted in experimental communities may preclude exotic species from invading (Funk et al., 2008; Hooper and Dukes, 2010). The setup provides a unique opportunity to study how functional trait-based restoration can promote diverse species assemblages using species not originally found at the site—including non-native but non-invasive species (Ewel and Putz, 2004; Schlaepfer et al., 2011). The non-native but non-invasive species were combined with natives to fill ecological roles that may have been lost or altered through human disturbance. In the Liko Nā Pilina Experiment (Fig. 2), the experimental treatments were planted communities (e.g., consisting of outplants) along with any previous native stems. Each treatment had the same species richness of outplanted trees ($n = 10$ outplant species per plot) but with different functional trait profiles (i.e., positions of species in trait space) based on two factors: (1) rates of expected carbon turnover (slow or moderate) because one objective of the restoration is to lower rates of invasion by decreasing carbon cycling rates (Hughes et al., 2014), and (2) the similarity of species in their functional trait measurements (redundant or complementary, as determined by functional dispersion calculations; Ostertag et al., 2015). The design resulted in four treatments (experimental communities): slow carbon redundant traits, moderate carbon redundant traits, slow carbon complementary traits, and moderate carbon complementary traits (Fig. 3). These treatments represent four experimental communities, each a combination of different management objectives. Each treatment had four replicate 20×20 m plots with a 5 m perimeter buffer, arranged in a randomized block design. A total of 20 species were incorporated into the experiment and were carefully chosen based on their expression of 15 functional traits (e.g., leaf C:N, maximum plant height, seed mass; see Table 1 in Ostertag
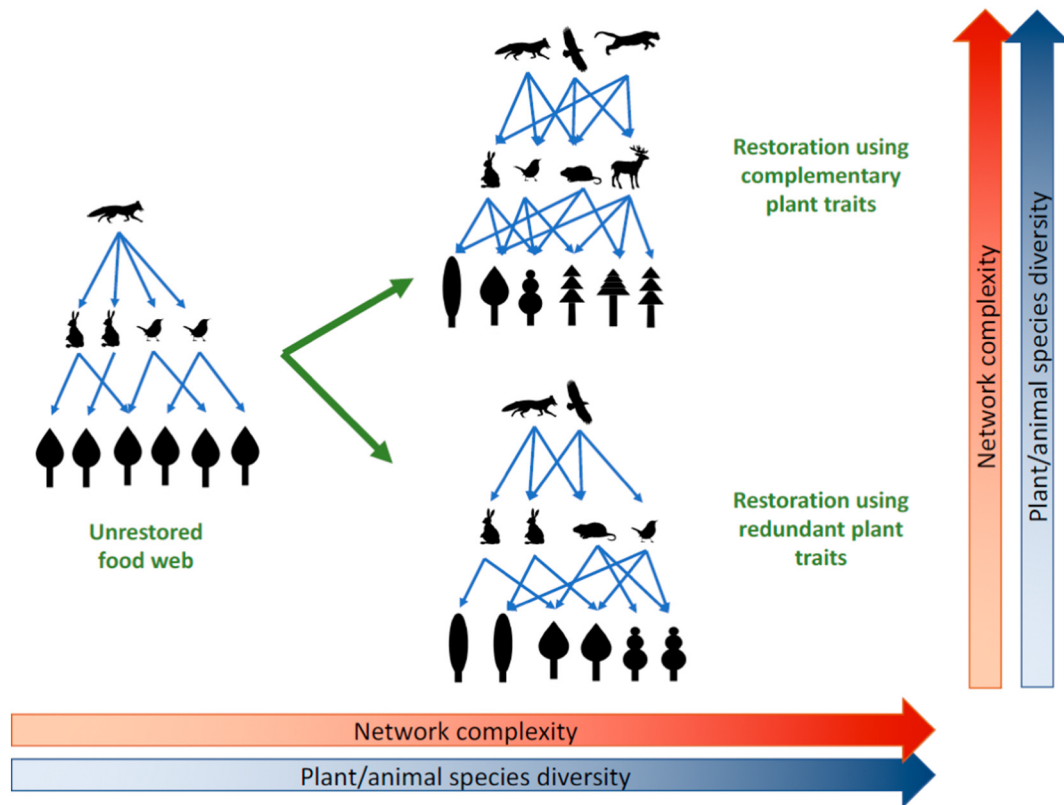
Fig. 1. A conceptual figure representing hypothesized mechanisms for how restoration using a functional trait approach can influence food webs by bottom-up effects. Different plant shapes represent species with a different combination of functional traits. Arrows link individuals from a trophic level that consume individuals from another trophic level. We represent food webs with three trophic levels: primary producers, primary consumers, and secondary consumers. Restoration efforts that increase the diversity of plant functional traits should have cascading effects on the food web, increasing animal diversity and network complexity. The increases in animal species and network complexity are expected to be stronger for restoration efforts using plants with complementary functional traits than those using plants with redundant traits.

et al. (2015)) and their non-invasive nature as determined by the Hawai'i Weed Risk Assessment (Daehler et al., 2004; Ostertag et al., 2015).

We examined the leaf litter arthropod community to address the hypotheses shown in Fig. 1. The young volcanic substrate (750–1500 yr) at the site has limited soil development, and previous research has shown that most nutrient cycling occurs through the leaf litter (Ostertag et al., 2009). Thus, we expected aboveground terrestrial food webs to be dominated by arthropods that can directly affect litter decomposition through comminution of plant material and grazing on bacteria and fungi (Seastedt, 1984; Moore et al., 1988). The initial data on leaf litter

arthropod communities and leaf litter decomposition rates at the site suggest links between the plant species and arthropod community composition and diversity. Litterfall has been collected ($n = 20$ litter trays per plot) monthly since the Liko Nā Pilina experiment's monitoring phase was initiated in 2014. We sorted and weighed by species to calculate outplant species contributions to changes in litterfall rates over time. Overall, between treatment comparisons were also made. In 2016, we conducted a decomposition experiment using litterfall collected on-site. We focused on both single species decomposition as well as mixed-litter (i.e., experimental community mix) decomposition.

Fig. 2. A plot in the Liko Nā Pilina experiment after initial planting (left) and after 3.5 years of growth (right). In the background are existing canopy trees and in the foreground are outplants. The rocky, volcanic substrate can be seen.
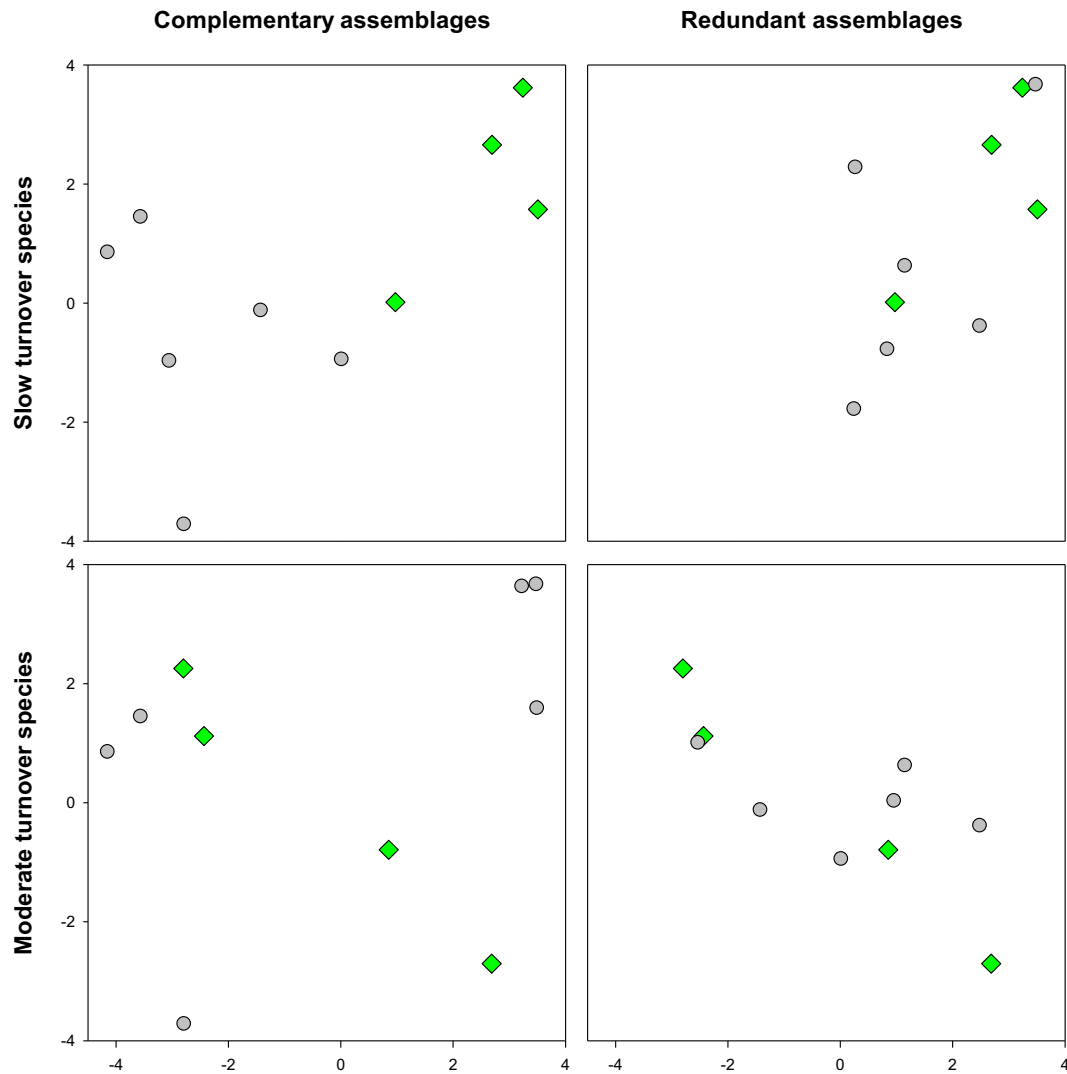
Complementary assemblages   **Redundant assemblages**

Fig. 3. The four experimental treatments of the Liko Nā Pilina restoration and community assembly experiment on Hawai'i Island. Each species position in 'trait space' was determined using principal components analysis. The core species were chosen from a previous principal components analysis that showed a distinct separation of species in terms rates of carbon turnover, and was primarily based on the following traits; leaf mass per area, carbon:nitrogen ratio, and foliar nitrogen concentrations. We selected core species to be either species with slow carbon turnover (i.e., associated with higher carbon storage) or moderate carbon turnover. Two native and two non-native core species were chosen for each treatment. Once these core species were designated (green diamonds), six additional species for each treatment (gray circles) were chosen to be near (redundant) or far (complementary) from the core species, based on calculations of the centroid.

Litter bags were constructed of 1 mm mesh fiberglass window screen, filled with 5 g of litter, and placed in the field sites. Bags ($n = 10$ per period per species and mixed litter treatments) were collected at intervals of 4 and 12 months. Decomposition rate constants (k values) were calculated for the single species and mixed litter treatments. Litterfall rates varied greatly (0–12.3 g/m^2/mo), as did decomposition rates (0.63–3.5 k) across individual plant species (Fig. 4a and b). At the experimental community level, litterfall rates were greater for the moderate redundant treatment than the two slow treatments with the moderate complementary treatment intermediate (ANOVA F$_{(3,16)}$ = 7.54, P = 0.0043; Fig. 4c). In comparison, decomposition rates were greater at the moderate complementary treatment than the moderate redundant treatment, with the two slow treatments intermediate (ANOVA F$_{(3,36)}$ = 4.04, P = 0.0149; Fig. 4d). All statistical results were evaluated with the criterion of $P < 0.05$.

These litter differences provided a template to investigate the litter arthropod community, of both microarthropods and macroarthropods. Microarthropods were the mites (Acari) and entognathids (primarily Collembola, but also Protura and Diplura), while macroarthropods included all arthropods not within these groups. In February 2019, we collected single leaf litter samples under canopies of 19 studied plant species to examine macroarthropod populations. This collection was the first of eight collections to be conducted quarterly and rotated across the four blocks twice. Collections per species were standardized by volume (i.e., one approximately 27 cm × 27 cm bag per species) and distributed spatially as evenly as possible across individuals planted per species in the four plots per block; small collections were made from beneath at least two individuals per species when possible. We identified 74 macroarthropod morphospecies, ranging between 17 and 35 per plant species. We also performed microarthropod collections as part of a June–July 2017 pilot study focusing on oribatid mites. Litter was collected from 11 tree species. We used four 25 cm^2 quadrats placed on the ground underneath the plant canopies and found 13 morphospecies of mites.

We investigated relationships among the arthropod community (both micro- and macroarthropods) and the plant functional traits using Redundancy Analyses (RDA) in R version 3.6.3 (2020-02-29) on an x86_64-apple-darwin15.6.0 (64-bit) platform (R Development Core, 2018). RDA ordinates invertebrate species using axes that are constrained to be linear combinations of the plant functional traits, in such a way that the relationship between the invertebrate species and the plant functional
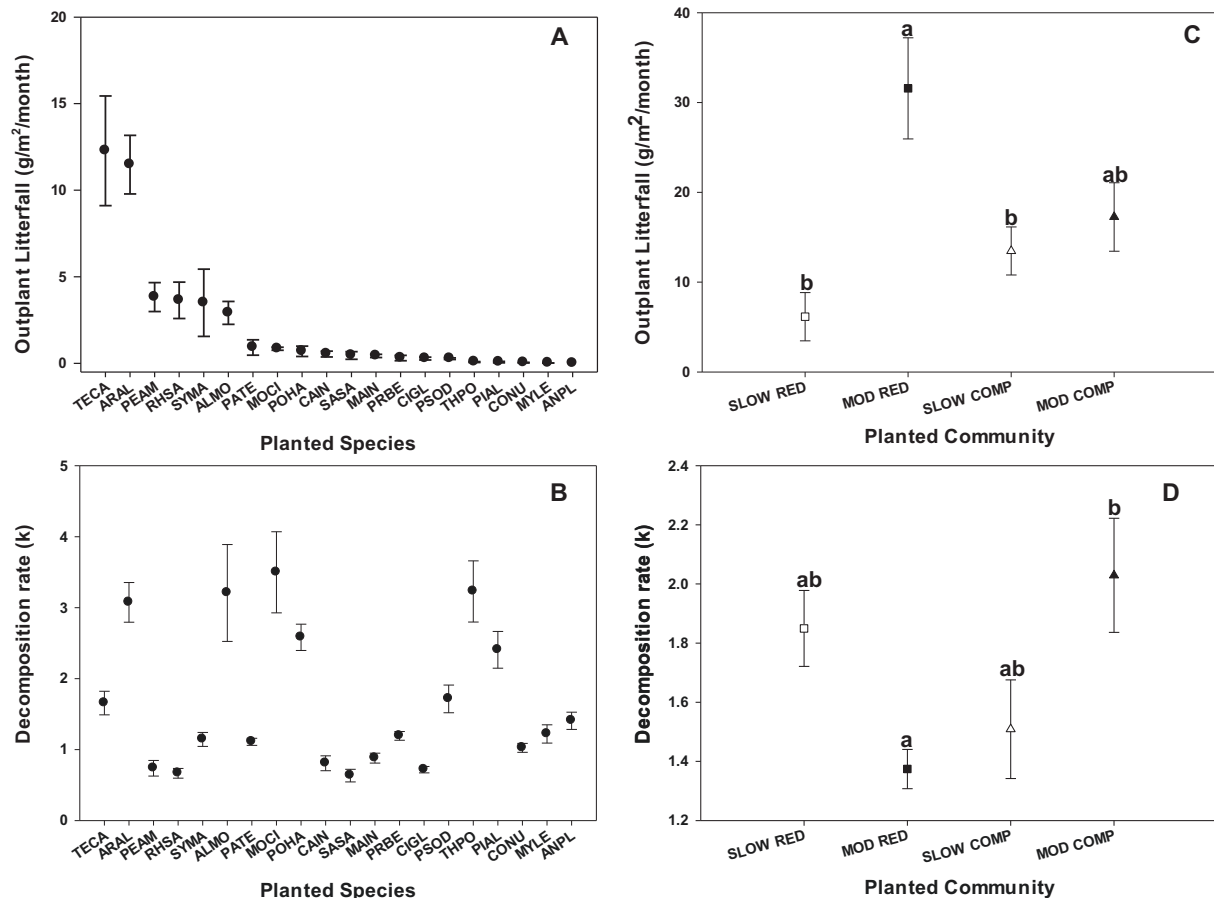
Fig. 4. The outplants in the experiment are diverging in ecosystem-level indices of litterfall and decomposition at both the individual species (A, B) and experimental community level (C, D). Planted species have been listed based on outplant litterfall (g/m²/month) contributions in descending order as follows: TECA (*Terminalia catappa*), ARAL (*Artocarpus altilis*), PEAM (*Persea americana*), RHSA (*Rhus sandwicensis*), SYMA (*Syzygium malaccense*), ALMO (*Aleurites moluccana*), PATE (*Pandanus tectorius*), MOCI (*Morinda citrifolia*), POHA (*Polyscias hawaiensis*), CAIN (*Calophyllum inophyllum*), SASA (*Samanea saman*), MAIN (*Mangifera indica*), PRBE (*Pritchardia beccariana*), CIGL (*Cibotium glaucum*), PSOD (*Psydrax odorata*), THPO (*Thespesia populnea*), PIAL (*Pipturus albidus*), CONU (*Cocos nucifera*), MYLE (*Myrsine lessertiana*), and ANPL (*Antidesma platyphyllum*). Planted communities have been listed as follows; SLOW RED (slow carbon redundant traits), MOD RED (moderate carbon redundant traits), SLOW COMP (slow carbon complementary traits), and MOD COMP (moderate carbon complementary traits). Values are means ± standard error. Differing letters indicate significant differences resulting from ANOVA followed by Tukey's multiple comparisons test.

traits can be seen. We started with the 15 functional traits data that were used to design the experimental treatments (Ostertag et al., 2015) and then ran a Variance Inflation Factor (VIF) analyses to look for collinearity. We eliminated all variables with a VIF > 10. Functional trait variables included in the RDA were foliar C and P concentrations, foliar δ^{13}C (a measure of integrated water-use efficiency), maximum plant height, seed mass, altitudinal range (a measure of habitat breadth), and shade ratio (a measure of the canopy architecture). While the taxonomic details of the arthropod data sets are still being worked out, RDA shows that the macroarthropod (Fig. 5a) and microarthropod (Fig. 5b) communities depend on the functional traits of the plant species and thus that primary consumers' functional traits affect the arthropod community. For macroarthropods, C concentration was the only significant variable ($P = 0.002$), which was tested by the distribution-free Monte Carlo test (999 permutations), in which the distribution of the test statistics under the null hypothesis is generated by random permutations of cases. For microarthropods, only height was significant ($P = 0.026$) and shade ratio was not significant but potentially important ($P = 0.098$).

4. Research questions that can take advantage of restoration projects

Given the importance of plant nutrient cycling in developing restoration projects, there are a variety of multi-trophic questions that could be investigated. Under a given climate or disturbance regime,

factors most strongly controlling leaf litter decomposition are litter quality (a combination of physical and chemical traits) and soil fauna (Heneghan et al., 1998; Powers et al., 2009; Meyer III et al., 2011; Paudel et al., 2015), and these two factors may interact with each other. For example, in a temperate forest, when plant litter diversity and soil animals were manipulated, the presence of soil fauna had a larger effect on decomposition rates for the more rapidly decomposing plant species (Hättenschwiler and Gasser, 2005). Plant species that exhibit leaf quality characteristics associated with faster decomposition rates (e.g., thinner leaves, lower C:N) may lead to greater rates of nutrient cycling during restoration. This higher nutrient availability is expected to influence arthropod density and biomass, as demonstrated in a Hawaiian montane forest study (Gruner, 2004). Thus, it is important to understand how decomposition rates affect consumers, in both less disturbed systems and during restoration.

Another opportunity for multi-trophic research occurs when considering plant community assembly. Functional complementarity could maximize the number of functional niches occupied, leading to increased diversity in available resource use and efficiency (Northfield et al., 2010). In contrast, functional redundancy will confer higher resilience to the community because the function of one species that is lost can be covered by redundant species (Walker, 1992, 1995). However, the principal mechanisms affecting complementary vs. redundant communities are still unclear (Tylianakis and Morris, 2017). A testable hypothesis is that for an equal number of species, plant communities
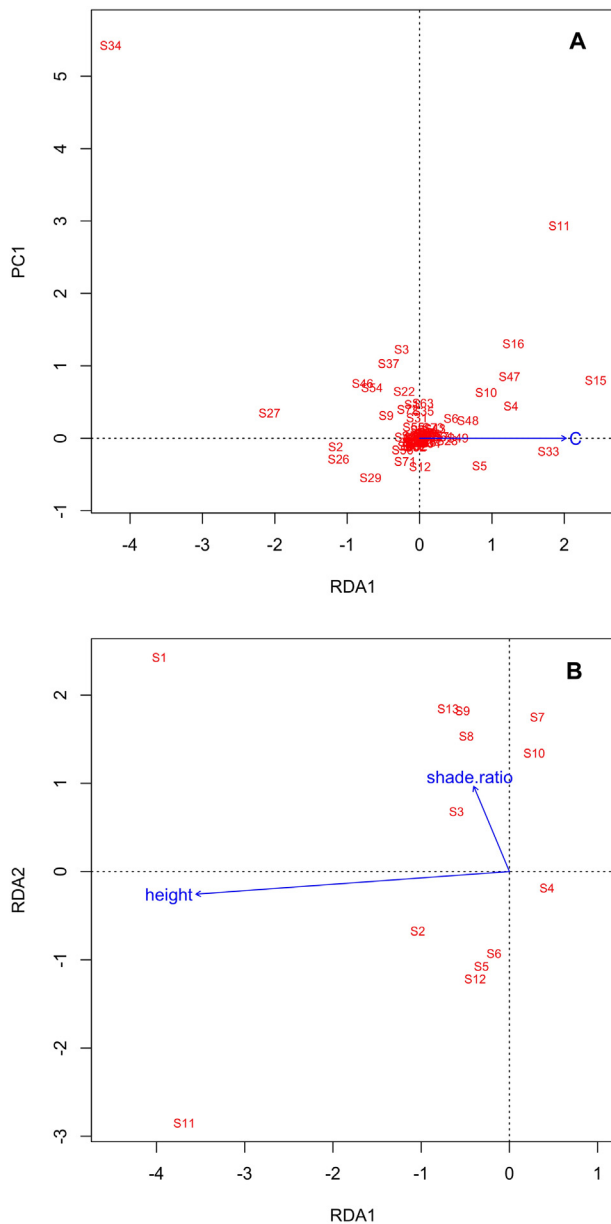
Fig. 5. Redundancy (RDA) analyses ordinating plant functional traits against macroarthropod (A) and microarthropod (B) morphospecies collected from leaf litter samples placed underneath plant species canopies that are planted in the Liko Nā Pilina experiment during periods of relative environmental similarity. Individual morphospecies are denoted as S1, S2, etc. and the vectors show the plant functional traits in the analysis. Arthropod abundance data were square-root transformed and all the plant functional traits were scaled before analysis. In (A), 74 morphospecies of macroarthropods were collected beneath 19 plant species and analyzed against the functional traits foliar C and P concentrations, foliar δ^{13}C (a measure of integrated water-use efficiency), maximum plant height, seed mass, altitudinal range (a measure of habitat breath), and shade ratio (a measure of the canopy architecture). C concentration was the only significant variable ($P = 0.002$). In (B), 13 microarthropod morphospecies were analyzed against foliar C and N concentrations, instantaneous water-use efficiency, leaf water content, maximum plant height, shade ratio, leaf mass per area, stem specific gravity, and stature (vertical position in the canopy). Only height was significant ($P = 0.026$) and shade ratio was marginally significant ($P = 0.098$).

with complementary traits (low niche overlap) provide more ecological niches for the higher trophic levels than those where some of the traits are redundant (high niche overlap) (Junker et al., 2015). The Liko Nā Pilina experiment has the design to provide a direct test of this hypothesis. More ecological niches can also be used by more functionally different animal species, increasing both animal diversity and functional diversity and our experimental design can also test this hypothesis, although it is dependent on which animal functional traits are quantified.

Also, plant, animal, and functional diversity values are likely to change over time, and the long-term temporal perspective is a linchpin of succession and restoration studies.

Plant functional trait composition can affect not only the species diversity but also the complexity of the interaction networks that are formed among the groups of species in the different trophic levels (Rzanny and Voigt, 2012). The study of interaction networks allows researchers to understand the dynamics and the mechanisms underlying community processes (Montoya et al., 2006; Thébault and Fontaine, 2010). It can be hypothesized that a greater number of ecological niches or greater nutrient availability may benefit the presence of specialized groups of species in plant communities with complementary traits, increasing the interaction diversity and specialization, and decreasing the connectance (i.e., proportion of realized interactions) of the network (Rzanny and Voigt, 2012).

Another interesting perspective is the quantification of the diversity of arthropod functional traits that are responsive to environmental drivers. For example, the body size of microarthropods is a significant indicator of environmental factors suggestive of climate change, such as warming temperature (Bokhorst et al., 2012) and drying of forest floors (Lindo et al., 2012). Similarly, oribatid mite and collembola communities have been shown to assemble differentially based on trophic position, reproductive strategy, and mobility following forest management practices differing in intensity (Farská et al., 2014). Litter arthropods can be examined from a functional perspective during restoration (Cole et al., 2016), linking plants and higher trophic levels. While traditional diversity measurements (e.g., species richness, diversity indices) are often informative in arthropod studies, the addition of trait-based metrics into community-level research will increase the analytical power needed to identify many subtle but important responses.

Finally, hypotheses can be developed that explore the interaction between nutrient availability and functional diversity. Meta-analysis has shown that leaf litter mixtures often decompose in a non-additive manner, either faster (synergistically) or slower (antagonistically) than expected (Gartner and Cardon, 2004). As with primary productivity, the number of plant species does not always correlate to the decomposition rate (Srivastava et al., 2009), suggesting that a functional diversity approach may be more informative. Litter mixtures that contain species more functionally dissimilar in physical and chemical traits are hypothesized to have synergistic effects (Schindler and Gessner, 2009; Lecerf et al., 2011). For example, Lecerf et al. (2011) found evidence for niche complementarity explaining differences in litter decomposition rate among litter mixtures in stream studies. Accordingly, the Resource Specialization Hypothesis (Hutchinson, 1959) suggests that increases in consumer diversity when plant diversity is high are caused by more plant species providing a greater quantity of resources and niches for the consumers (Haddad et al., 2009; Scherber et al., 2010; Schuldt et al., 2015). Because restoration ecologists often design experiments in such a way that resource availability will change over time (e.g., plantings that lead to shading, bird visitation, or increased soil water), planning for functionally diverse litter inputs could become an important management strategy.

5. Broadening the concept of functional restoration

Developing restoration projects based on plant functional traits that influence both plant and invertebrate species provides a new design paradigm. It encourages going one step further from restoring biodiversity to restoring ecosystems where lost ecological functions are reintroduced. However, long-term restoration efforts add much to our knowledge about the stability, resilience, or interspecific interactions, of restored ecosystems (Allsopp et al., 2008; Martín-López et al., 2014; Ma et al., 2016). Most of the terrestrial biodiversity and ecosystem function experiments and higher-level trophic studies to date have been in simplified systems —mainly grasslands (Koricheva et al., 2000). However, restoration needs are global and varied. Forest ecosystems are understudied, partly due to

the logistical challenges and time needed for manipulating large woody species (Zavaleta et al., 2001). Also, in some places, such as the Liko Nā Pilina Experiment in Hawai'i, restoration creates hybrid ecosystems (i.e., that contain both native and non-native but non-invasive plants, Hobbs et al., 2014). The rationale for this approach is that it is not feasible to return to a previous state for reasons that include the lack of reference sites or historical baseline conditions, irreversible climate change, and colonization by non-native species that cannot practically or economically be removed (Zedler et al., 2012; Hobbs et al., 2014). An important consideration is that hybrid ecosystem restoration will likely contain more animal inhabitants that are non-native, providing an opportunity for new types of species interactions, such as mutualisms (Ewel and Putz, 2004), leading to broader philosophic discussions of native and non-native species and human impacts (Robbins and Moore, 2013). Overall, shifting from the "if you build it, they will come" strategy toward a functional restoration approach that affects the entire food web can provide greater insights about how to improve outcomes. Long-term restoration projects, from grasses to trees, which consider new types of community assemblages when the original ones cannot be recovered could be valuable in restoration efforts.

Funding

Data availability

Data are available at Ostertag, Rebecca (2020), "Food Webs Prelim Arthropod Data", Mendeley Data, V1, doi:10.17632/gw3rcd3769.1.

CRediT authorship contribution statement

Rebecca Ostertag: Conceptualization, Methodology, Formal analysis, Writing—Original draft preparation, Resources. **Esther Sebastian:** Conceptualization, Software, Formal analysis, Writing—Original draft preparation. **Robert Peck:** Conceptualization, Methodology, Writing—Original draft preparation, Resources. **Trebor Hall:** Methodology, Formal analysis, Investigation, Data curation, Writing—reviewing and editing. **Jihoo Kim:** Investigation, Data curation, Writing—reviewing and editing. **Nicole DiManno:** Methodology, Formal analysis, Investigation, Data curation, Writing—reviewing and editing. **Donald Rayome:** Writing—Original draft preparation, Conceptualization, Investigation, Resources. **Susan Cordell:** Conceptualization, Writing—Original draft preparation, Resources. **Paul Banko:** Conceptualization, Writing—reviewing and editing, Resources. **Amanda Uowolo:** Writing—reviewing and editing.

Declaration of competing interest

None.

Acknowledgments

References

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., Hillebrand, H., 2011. More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. P. Natl. Acad. Sci. USA. 108, 17034–17039.

Allsopp, M.H., de Lange, W.J., Veltman, R., 2008. Valuing insect pollination services with cost of replacement. PLoS One 3, 1–8.

Bhaskar, R., Dawson, T.E., Balvanera, P., 2014. Community assembly and functional diversity along succession post-management. Funct. Ecol. 28, 1256–1265.

Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. Glob. Chang. Biol. 18, 1152–1162.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., et al., 2011. The functional role of producer diversity in ecosystems. Am. J. Bot. 98, 572–592.

Chillo, V., Ojeda, R.A., Capmourteres, V., Anand, M., 2017. Functional diversity loss with increasing livestock grazing intensity in drylands: the mechanisms and their consequences depend on the taxa. J. Appl. Ecol. 54, 986–996.

Cole, R.J., Holl, K.D., Zahawi, R.A., Wickey, P., Townsend, A.R., 2016. Leaf litter arthropod responses to tropical forest restoration. Ecol. Evol. https://doi.org/10.1002/ece3.2220.

Cordell, S., Ostertag, R., Michaud, J., Warman, L., 2016. Quandaries of a decade long restoration experiment trying to reduce invasive species: beat them, join them, give up, or start over? Restor. Ecol. 24, 139–144.

Craven, D., Isbell, F., Manning, P., Connolly, J., Bruelheide, H., Ebeling, A., et al., 2016. Plant diversity effects on grassland productivity are robust to both nutrient enrichment and drought. Philos. T. R. Soc. B 371, 20150277. https://doi.org/10.1098/rstb.2015.0277.

Daehler, C.C., Denslow, J.S., Ansari, S., Kuo, H., 2004. A risk assessment system for screening out invasive pest plants from Hawai'i and other Pacific Islands. Conserv. Biol. 18, 360–368.

Deraison, H., Badenhausser, I., Loeuille, N., Scherber, C., Gross, N., 2015. Functional trait diversity across trophic levels determines herbivore impact on plant community biomass. Ecol. Lett. 18, 1346–1355.

Devoto, M., Bailey, S., Craze, P., Memmott, J., 2012. Understanding and planning ecological restoration of plant–pollinator networks. Ecol. Lett. 15, 319–328.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. P. Natl. Acad. Sci. USA 104, 20684–20689.

Dinnage, R., Cadotte, M.W., Haddad, N.M., Crutsinger, G.M., Tilman, D., 2012. Diversity of plant evolutionary lineages promotes arthropod diversity. Ecol. Lett. 15, 1308–1317.

Ewel, J.J., Putz, F.E., 2004. A place for alien species in ecosystem restoration. Front. Ecol. Environ. 2, 354–360.

Farská, J., Prejzková, K., Rusek, J., 2014. Management intensity affects traits of soil microarthropod community in montane spruce forest. Appl. Soil Ecol. 75, 71–79.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., et al., 2009. Leaf traits capture the effects of land use and climate on litter decomposability of herbaceous communities across Europe. Ecology 90, 598–611.

Fraser, L.H., Harrower, W.L., Garris, H.W., Davidson, S., Hebert, P.D.N., Howie, R., et al., 2015. A call for applying trophic structure in ecological restoration. Restor. Ecol. 23, 503–507.

Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S., 2008. Restoration through reassembly: plant traits and invasion resistance. Trends Ecol. Evol. 23, 695–703.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gartner, T.B., Cardon, Z.G., 2004. Decomposition dynamics in mixed-species leaf litter. Oikos 104, 230–246.

Gillison, A.N., Bignell, D.E., Brewer, K.R.W., Fernandes, E.C.M., Jones, D.T., Sheil, D., et al., 2013. Plant functional types and traits as biodiversity indicators for tropical forests: two biogeographically separated case studies including birds, mammals and termites. Biodivers. Conserv. 22, 1909–1930.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Gruner, D.S., 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85, 3010–3022.

Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M., Knops, J., 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. Am. Nat. 158, 17–35.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, K., Knops, J.M.H., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecol. Lett. 12, 1029–1039.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. PNAS 102, 1519–1524.

Heneghan, L., Coleman, D.C., Zoub, X., Crossley, D.A., Haines, B.L., 1998. Soil microarthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites. Appl. Soil Ecol. 9, 33–38.

Hertzog, L.R., Meyer, S.T., Weisser, W.W., Ebeling, A., 2016. Experimental manipulation of grassland plant diversity induces complex shifts in aboveground arthropod diversity. PLoS One 11, e0148768. https://doi.org/10.1371/journal.pone.0148768.

Hobbs, R.J., Higgs, E.S., Harris, J.A., 2014. Novel ecosystems: concept or inconvenient reality? A response to Murcia et al. Trends Ecol. Evol. 29, 645–646.

Hooper, D.U., Dukes, J.S., 2010. Functional composition controls invasion success in a California serpentine grassland. J. Ecol. 98, 764–777.

Hughes, R.F., Asner, G.P., Mascaro, J., Uowolo, A., Baldwin, J., 2014. Carbon storage landscapes of lowland Hawaii: the role of native and invasive species through space and time. Ecol. Appl. 24, 716–731.

Hutchinson, G., 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93, 145–159.

Junker, R.R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, H.M., Stang, M., 2013. Specialization on traits as basis for the niche- breadth of flower visitors and as structuring mechanism of ecological networks. Funct. Ecol. 27, 329–341.

Junker, R.R., Blüthgen, N., Keller, A., 2015. Functional and phylogenetic diversity of plant communities differently affect the structure of flower-visitor interactions and reveal convergences in floral traits. Evol. Ecol. 29, 437–450.

Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J., Huss-Danell, K., 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. Oecologia 125, 271–282.

Kuppler, J., Höfers, M.K., Wiesmann, L., Junker, R.R., 2016. Time-invariant differences between plant individuals in interactions with arthropods correlate with intraspecific variation in plant phenology, morphology and floral scent. New Phytol. 210, 1357–1368.

Laughlin, D., 2011. Nitrification is linked to dominant leaf traits rather than functional diversity. J. Ecol. 99, 1091–1099.

Laureto, L.M., Cianciaruso, M., Samia, D.S.M., 2015. Functional diversity: an overview of its history and applicability. Nat. Conservacao 13, 112–116.

Lecerf, A., Marie, G., Kominoski, J.S., LeRoy, C.J., Bernadet, C., Swan, C., 2011. Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. Ecology 92, 160–169.

Lefcheck, J.S., Duffy, J.E., 2015. Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. Ecology 96, 2973–2983.

Lindo, Z., Whiteley, J., Gonzalez, A., 2012. Traits explain community disassembly and trophic contraction following experimental environmental change. Glob. Chang. Biol. 18, 2448–2457.

Ma, S., Duggan, J.M., Eichelberger, B.A., McNally, B.W., Foster, J.R., Pepi, E., Conte, M.N., Daily, G.C., Ziv, G., 2016. Valuation of ecosystem services to inform management of multiple-use landscapes. Ecosyst. Serv. 19, 6–18.

Martín-López, B., Gómez-Baggethun, E., García-Llorente, M., Montes, C., 2014. Trade-offs across value-domains in ecosystem services assessment. Ecol. Indic. 37, 220–228.

Meyer III, W.M., Ostertag, R., Cowie, R.H., 2011. Macro-invertebrates accelerate litter decomposition and nutrient release in a young Hawaiian rainforest. Soil Biol. Biochem. 43, 206–211.

Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. Nature 442, 259–264.

Moore, J.C., Walter, D.E., Hunt, H.W., 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Annu. Rev. Entomol. 33, 419–439.

Northfield, T.D., Snyder, G.B., Ives, A.R., Snyder, W.E., 2010. Niche saturation reveals resource partitioning among consumers. Ecol. Lett. 13, 338–348.

Ostertag, R., Cordell, S., Michaud, J., Cole, T.C., Schulten, J.R., Publico, K.M., Enoka, J.H., 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. Ecosystems 12, 503–515.

Ostertag, R., Warman, L., Cordell, S., Vitousek, P.M., 2015. Using plant functional traits to restore Hawaiian rainforest. J. Appl. Ecol. 52, 805–809.

Paudel, E., Dossa, G.G.O., de Blécourt, M., Beckschäfer, P., Xu, J., Harrison, R.D., 2015. Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere. 6, 1–20. https://doi.org/10.1890/ES15-00112.1.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Powers, J.S., Montgomery, R.A., Adair, E.C., Brearley, F.Q., DeWalt, S.J., Castanho, C.T., et al., 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J. Ecol. 97, 801–811.

Qian, H., 2007. Relationships between plant and animal species richness at a regional scale in China. Conserv. Biol. 21, 937–944.

R Development Core, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna www.R-project.org (accessed 27 March 2020).

Rayome, D.D., Ostertag, R., Cordell, S., 2018. Enhancing aboveground carbon storage and invasion resistance through restoration: early results from a functional trait-based experiment. Pac. Sci. 72, 149–164.

Rayome, D.D., Ostertag, R., Cordell, S., Vitousek, P., Fung, B., Pante, P., Tate, R., Vizzone, A., 2019. Restoring Ecosystem Services Tool (REST) Introduction and User Guide. Gen. Tech. Rep. PSW-GTR-262. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.

Robbins, P., Moore, S.A., 2013. Ecological anxiety disorder: diagnosing the politics of the Anthropocene. Cult. Geogr. 20, 3–19.

Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. Science https://doi.org/10.1126/science.1253497.

Rzanny, M., Voigt, W., 2012. Complexity of multitrophic interactions in a grassland ecosystem depends on plant species diversity. J. Anim. Ecol. 81, 614–627.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., et al., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.

Schindler, M.H., Gessner, M.O., 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. Ecology 90, 1641–1649.

Schittko, C., Hawa, M., Wurst, S., 2014. Using a multi-trait approach to manipulate plant functional diversity in a biodiversity-ecosystem function experiment. PLoS One 9, e99065. https://doi.org/10.1371/journal.pone.0099065.

Schlaepfer, M.A., Sax, D.F., Olden, J.D., 2011. The potential conservation value of nonnative species. Conserv. Biol. 25, 428–437.

Schleuter, D., Daufresne, M., Massol, F., Argillier, C., 2010. A user's guide to functional diversity indices. Ecol. Monogr. 80, 469–484.

Schuldt, A., Both, S., Bruelheide, H., Härdtle, W., Schmid, B., Zhou, H., Assmann, T., 2011. Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS One 6, e22905. https://doi.org/10.1371/journal.pone.0022905.

Schuldt, A., Wubet, T., Buscot, F., Staab, M., Assmann, T., Böhnke-Kammerlander, M., 2015. Multitrophic diversity in a biodiverse forest is highly nonlinear across spatial scales. Nat. Commun. 6. https://doi.org/10.1038/ncomms10169.

Schuldt, A., Ebeling, A., Kunz, M., et al., 2019. Multiple plant diversity components drive consumer communities across ecosystems. Nat. Commun. 10, 1460. https://doi.org/10.1038/s41467-019-09448-8.

Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. Annu. Rev. Entomol. 29, 25–46.

Šipoš, J., Hédl, R., Hula, V., Chudomelová, M., Košulič, O., Niedobová, J., Riedl, V., 2017. Patterns of functional diversity of two trophic groups after canopy thinning in an abandoned coppice. Folia Geobot 52, 45–58.

Spake, R., Barsoum, N., Newton, A.C., Doncaster, P., 2016. Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. For. Ecol. Manag. 359, 300–308.

Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., Wright, J.P., 2009. Diversity has stronger top-down than bottom-up effects on decomposition. Ecology 90, 1073–1083.

Thébault, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329, 853–856.

Tilman, D., Reich, P.B., Knops, J.M.H., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441, 629–632.

Tylianakis, J.M., Morris, R.J., 2017. Ecological networks across environmental gradients. Annu. Rev. Ecol. Evol. Syst. 48, 25–48.

Vander Zanden, J., Olden, J.D., Gratton, C., 2006. Food-web approaches in restoration ecology. In: Falk, D.A., Palmer, M.A., Zedler, Z.B. (Eds.), Foundations of Restoration Ecology. Island Press, Washington, DC, pp. 165–189.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.

Walker, B.H., 1992. Biodiversity and ecological redundancy. Conserv. Biol. 6, 18–23.

Walker, B.H., 1995. Conserving biological diversity through ecosystem resilience. Conserv. Biol. 9, 747–752.

Wright, J., Symstad, A., Bullock, J.M., Engelhardt, K., Jackson, L., Bernhardt, E., 2009. Restoring biodiversity and ecosystem function: will an integrated approach improve results? In: Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (Eds.), Biodiversity, Ecosystem Functioning and Human Wellbeing. Oxford University Press, Oxford, UK, pp. 167–177

Zavaleta, E., Hobbs, R.J., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol. Evol. 16, 454–459.

Zedler, J.B., Doherty, J.M., Miller, N.A., 2012. Shifting restoration policy to address landscape change, novel ecosystems, and monitoring. Ecol. Soc. 17, 36. www.ecologyandsociety.org/vol17/iss4/art36/ (accessed 27 March 2020).