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ECOLOGICAL NETWORKS

Structure, spatial dynamics, and stability of novel seed dispersal mutualistic networks in Hawai'i

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Increasing rates of human-caused species invasions and extinctions may reshape communities and modify the structure, dynamics, and stability of species interactions. To investigate how such changes affect communities, we performed multiscale analyses of seed dispersal networks on O'ahu, Hawai'i. Networks consisted exclusively of novel interactions, were largely dominated by introduced species, and exhibited specialized and modular structure at local and regional scales, despite high interaction dissimilarity across communities. Furthermore, the structure and stability of the novel networks were similar to native-dominated communities worldwide. Our findings suggest that shared evolutionary history is not a necessary process for the emergence of complex network structure, and interaction patterns may be highly conserved, regardless of species identity and environment. Introduced species can quickly become well integrated into novel networks, making restoration of native ecosystems more challenging than previously thought.

High rates of human-caused species invasions and extinctions are a ubiquitous feature of the Anthropocene (*1*, *2*). As a result, "novel communities" have emerged, characterized by a reshuffling of species, changes in species interactions, and, in some cases, alteration or disruption of ecosystem services maintained by these interactions (*3*, *4*). Mutualistic plant-animal networks are particularly susceptible to species loss (*5*) and invasions (*4*, *6*, *7*), increasing the vulnerability of species and communities to further perturbations (*4*). Previous studies have focused on native-dominated communities in which few or no invasive species occur and mutualistic partners have interacted for prolonged periods of time, developing complex and often coevolved interactions (*8*, *9*). By contrast, the architecture and stability of novel interaction networks across spatial scales and how they compare to native-dominated communities remain virtually unknown. This knowledge gap hampers our ability to forecast and mitigate the impacts of extinctions and invasions on ecosystem functions.

Here we address these gaps by examining the structure, dynamics, and stability to perturbations of multiple novel communities in the Hawaiian archipelago and compare our results with networks from communities worldwide. Hawai'i provides an opportunity to investigate the consequences of an extreme scenario of loss of native species and their replacement by non-native species. Most native Hawaiian forest plants are bird-dispersed, yet no native dispersers remain in most ecosystems (*10*, *11*). Thus, seed dispersal is almost entirely dependent on a handful of introduced vertebrate dispersers, nearly all of which are birds (*10*, *11*). O'ahu, in particular, is among the areas most affected by extinctions and biological invasions in the world (*12*): All its native frugivores are extinct.

To what extent are introduced species integrated into seed dispersal networks (SDNs), and do introduced dispersers replace extinct native animals? To investigate these questions, we examined interactions based on 3278 fecal samples from 21 bird species [tables S1 to S3 and (*13*)] collected over 3 years at seven sites encompassing broad environmental variation across O'ahu (fig. S1 and table S1). We identified 109,424 viable seeds, representing 1792 seed dispersal events (presence of viable seeds in a sample). O'ahu's SDN included 15 bird and 44 plant species connected by 112 distinct links (Fig. 1). Most birds (86.7%) and plants (65.9%) are not native to Hawai'i; introduced plants accounted for 93.3% of dispersal events, and there was no interaction between a native bird and a native plant. Proportions of introduced species varied from 60.0 to 100% for birds and 50.0 to 100% for plants, two local networks consisted entirely of introduced species, and the number of species and links was highly variable across sites (table S4). We found that 59.0% of fecal samples contained seeds (table S4), but only 0.22% of interactions (n = 4 events) involved native birds (two species not specialized for fruit consumption). Thus, although introduced birds are critical for seed dispersal in the ecosystem, they are primarily dispersing introduced plants (only 6.7% of interactions involved native plants).

We assessed species interaction patterns via complex network analyses and used four complementary metrics known to vary geographically and reflect community-level responses to major drivers of biodiversity patterns, such as productivity, climatic seasonality, and historical climatic stability [e.g., (*14*–*16*)]. A network is an interaction matrix for which each row i is a plant species and each column j is a bird species, with intersections a_{ij} describing interaction intensity. The statistical significance of the observed topological patterns was assessed by contrasting observed values for each metric with the confidence interval from null models (*13*). Like other mutualistic networks, SDNs in native-dominated communities typically have consistent structures: (i) low connectance—not all possible interactions are realized; (ii) high specialization—few supergeneralist species exist and most species interact with a few partners in a complementary way; (iii) nested topology—specialist species tend to interact with subsets of partners of the most generalist species; and (iv) modular structure—subsets of species interacting preferentially with each other, forming modules of highly connected species (*17*–*20*).

Novel insular communities are predicted to have low specialization because of niche broadening (*21*) and interaction release (*22*). For example, both fleshy-fruited plants and frugivores on islands tend to have wide niches owing to resource limitation (*4*). Consequently, high connectance and nonmodular structures are expected, because both are linked to low specialization [e.g., (*14*, *23*)]. For nestedness, contrasting predictions exist because low specialization can either lead to non-nested topology, owing to random partners associating, or to nested topology, driven by species' relative abundances, which defines probabilities of species encountering one another (*20*, *24*). In contrast to theoretical predictions, we found that O'ahu networks were nonrandom and had highly complex structures at local (site-specific) and regional (island-wide) scales. The regional network had low connectance, moderate specialization, and nested and modular topologies, with three distinct modules (Fig. 1, fig. S2, and table S4). At the local scale, networks had low to intermediate connectance and, unlike the regional network, were not nested. Similar to the regional network, six of seven local networks were specialized and modular, presenting three or four modules (Fig. 2, fig. S3, and table S4). We found that despite all interactions being novel and primarily involving introduced species, networks were structurally complex and notably similar between scales (local versus regional) and across sites. Furthermore, partner sharing (how distinct species share resources) in SDNs on O'ahu is structured in a complementary way among bird and plant species, giving rise to distinct modules in which certain birds and plants

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interact preferentially. The emergence of such structures indicates that these novel SDNs largely reproduce the well-known patterns exhibited in mutualistic networks (*18*) and that SDN structure is highly conserved, regardless of variation in plant and bird communities. Given the low generalization in our novel insular networks, interaction release (*22*) either is not occurring or may occur in the form of consumption of more food types (e.g., insects, fruits, and nectar), rather than increased diversity within a specific resource type (e.g., greater number of species of fruits).

Several studies suggest that the phylogenetic relationships of species contribute to structuring mutualistic networks [e.g., (*25*, *26*)], which is an expected consequence of coevolved interactions among species interacting for prolonged (evolutionary) periods of time (*8*). Here we show that the interaction patterns recurrently identified in native-dominated networks also emerge in novel mutualistic networks composed of species with little or no shared evolutionary history. This result indicates that prolonged shared evolutionary history is not necessary for the emergence of complex network structure. We should note, however, that preexisting adaptations of introduced birds for frugivory and fruits for bird dispersal are necessary for their integration into novel networks. Furthermore, the presence of nested structure at regional, but not local, scale indicates the critical importance of spatial scale to understanding network patterns and their underlying processes. The wider variety of partners used at the larger scale (regional network) corresponds to the "fundamental niche," whereas the subset of partners found at local scales indicates that local populations have much more restricted "realized niches" (*27*, *28*). Therefore, not all species use available resources in the same way across all sites. By sampling across large spatial scales, researchers may be evaluating species' fundamental niches and not population-level realized niches. Therefore, processes operating at different spatial scales may be overlooked or confounded (*27*, *28*).

Most networks have been studied primarily as static entities at single sites, despite the importance of multiscale studies for understanding the processes underlying network structure and for evaluating the generalizability of network patterns (*29*). To examine interaction dynamics across sites and to test their association with environmental variables, we calculated the dissimilarity (interaction turnover) between pairs of networks, using data limited to species present in the networks. Highest dissimilarity occurs when two sites share no interactions. We decomposed this metric into two components: species turnover (β_{ST}—the proportion of interactions that are not shared owing to differences in species composition between two networks) and linkage turnover [β_{OS}, also called rewiring—the proportion of interactions unique to a single network despite the occurrence of both partners in both networks (*30*)].

We found high interaction dissimilarity among sites owing to both changes in species composition and rewiring. This suggests high flexibility

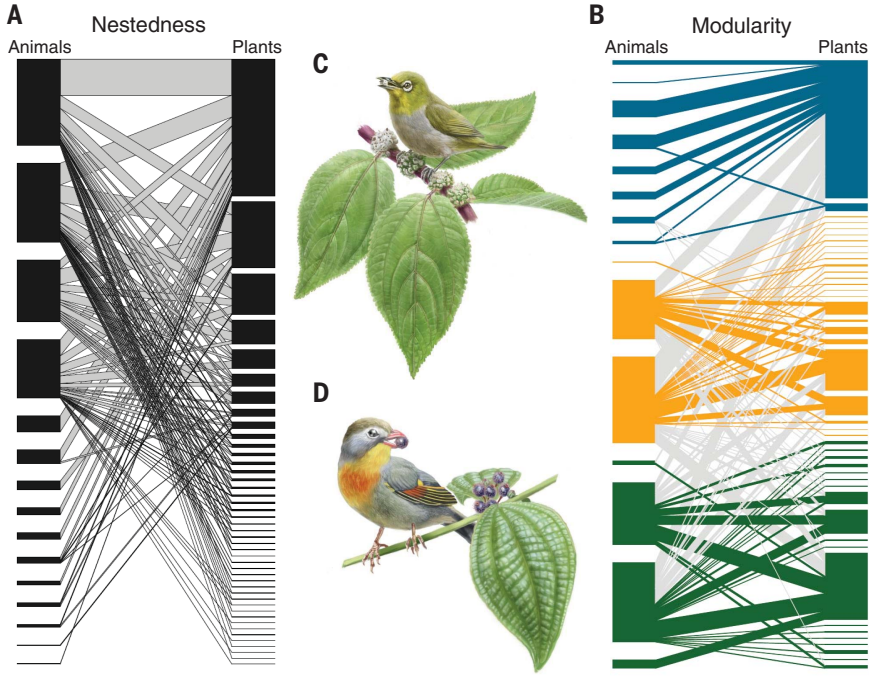

Fig. 1. Structure of the island-wide seed dispersal network on O'ahu and illustration of two emblematic interactions. (**A** and **B**) The novel network was nested [specialist species interacting with proper subsets of partners of the most generalist species (wNODF) = 48.67; 95% confidence interval (CI) = 34.24 to 46.66] (A) and modular [subsets of species interacting preferentially with each other, forming modules of highly connected species (Q_W) = 0.24; 95% CI = 0.07 to 0.09] (B). Species and links from distinct modules are depicted by different colors (blue, orange, and green), and gray links are interactions connecting modules. For a list of interacting species, see fig. S2. (**C**) Japanese white-eye feeding on *Pipturus albidus*, the most commonly consumed native plant. (**D**) A red-billed leiothrix feeding on *Clidemia hirta*, the most widely consumed and widespread introduced plant. [Illustration credit: P. Lorenzo]

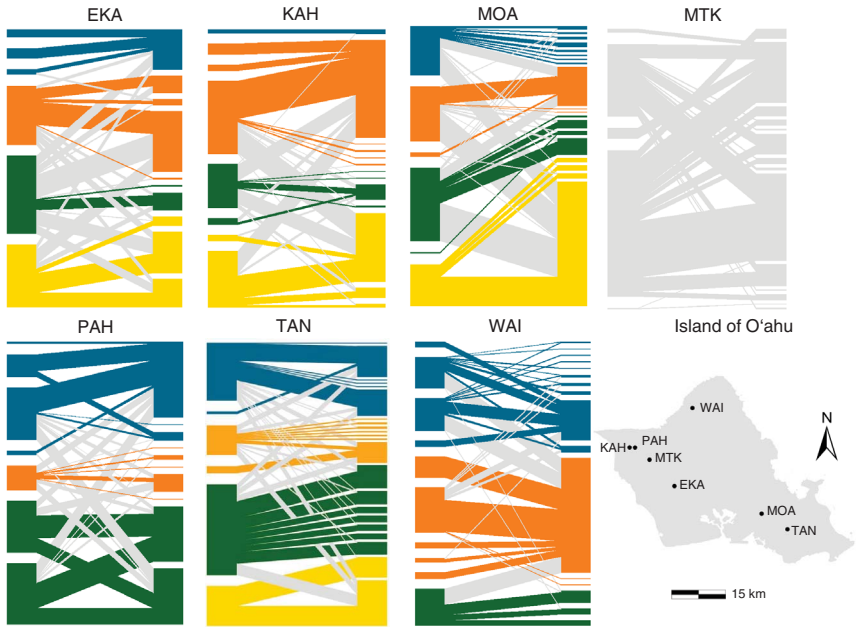

Fig. 2. Local SDNs on O'ahu. Each of the seven networks includes all birds (left side of network) and plants (right side of network) consumed in a specific site. Blue, orange, green, and yellow depict modules with species interacting more among themselves than with other species, as identified by Beckett's algorithm (*33*). All local networks but MTK were modular, presenting three or four modules. Line thickness indicates frequency of interactions. For a list of interacting species, see fig. S3. EKA, 'Ēkahanui; KAH, Kahanahāiki; MOA, Moanalua; MTK, Mount Ka'ala; PAH, Pahole; TAN, Tantalus; WAI, Waimea Valley.

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of birds and plants to switch partners, which is a major characteristic of highly successful invasive species (*31*). Interaction turnover across sites was high [interaction dissimilarity (β_{WN}) = 0.57 ± 0.11, mean ± SE; n = 21 pairwise sites; Fig. 3 and table S5], indicating that, on average, only 43% of interactions were shared between sites despite the most common bird and plant species occurring at all sites (tables S2 and S3). Surprisingly, only 53% of the interaction dissimilarity was due to differences in species composition among sites (β_{ST} = 0.30 ± 0.09), whereas 47% was because pairs of species that interacted in one site did not interact in another site where they co-occurred (β_{OS} = 0.27 ± 0.07; fig. S4). This indicates that, in addition to its influence on the structure of mutualistic networks [i.e., nestedness; (*32*)], partner switching is a major component of the spatial dynamics of novel networks. High interaction dissimilarity has also been reported in specialized, native-dominated pollination networks, even between spatially close networks (*33*). Thus, plant-animal networks appear to have distinct links (high interaction rewiring) even when the same species are present in both sites, irrespective of whether networks are dominated by native or introduced species.

Abiotic factors had a greater effect than biotic factors on the overall interaction dissimilarity and the dissimilarity caused by species turnover between sites, whereas interaction rewiring was not influenced by any factor examined (tables S6 to S11). Specifically, interaction dissimilarity and the dissimilarity caused by species turnover were influenced by elevation and rainfall, but not by percent of introduced plant species (tables S6 to S9). This suggests that the environment indirectly influences interactions via effects on species distributions, including the distribution of introduced species. However, the lack of association between rewiring and examined factors indicates that birds and plants in the system are highly flexible and can switch partners, irrespective of abiotic conditions and the identity of species in the community.

Lastly, we compared O'ahu SDNs with native-dominated SDNs around the world and found that O'ahu's novel networks resemble the structure and stability of native-dominated networks. We assembled and analyzed a dataset of 42 avian SDNs encompassing a broad geographical range, with data from islands (n = 17) and continents (n = 25) in tropical (n = 18) and nontropical (n = 24) areas (table S12). Although some of the other SDNs in the analyses included introduced species [e.g., (*7*, *34*)], SDNs on O'ahu present an extreme case of dominance by introduced species (>50%), coupled with extinction of all native frugivorous birds. For these 42 networks and the seven on O'ahu, we calculated a set of weighted (for 26 networks where frequency of interaction was reported) and binary (for all 42 networks) descriptors of network structure. We also estimated robustness (stability to species loss) of each network as the rate of secondary extinction expected under the simulated loss of network partners, assuming a species goes extinct when all connected partners are lost (*35*, *36*). We estimated robustness of animals to the extirpation of plants (assuming bottom-up control) and robustness of plants to the extirpation of animals (top-down control). We simulated two scenarios, one in which order of extirpation was random and another—more extreme—scenario in which order was from the most generalist to the most specialist species. After using a null model correction on each metric to account for variation in sampling intensity and network dimensions across studies (*14*), we compared the 95% confidence intervals for the O'ahu networks with the global dataset. We found that specialization, modularity, nestedness, and the simulated robustness in all scenarios to species loss of the O'ahu networks overlapped with the range of values observed in other networks. These results held true for both weighted and binary data and when O'ahu's networks were compared to subsets of networks from tropical and nontropical islands and continents. The only exceptions were that the specialization and weighted modularity observed in O'ahu networks were lower than those in networks from nontropical continental areas (Fig. 4 and table S13).

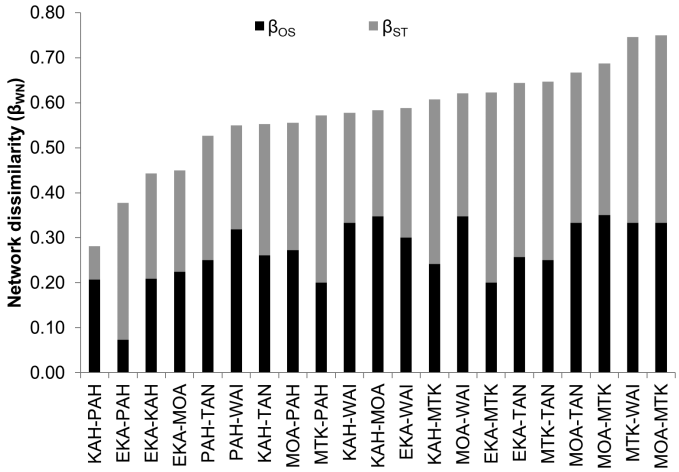

Fig. 3. Interaction dissimilarity between each pair of sites on O'ahu. Interaction dissimilarity (β_{WN}) was decomposed into its two components: species turnover (β_{ST}) and linkage turnover among species shared by pairwise sites (i.e., rewiring, β_{OS}).

Most SDNs from communities around the world have been described as specialized, nested, and modular [e.g., (*19*)], and the variation in such structures reveals the responses of species interactions to biotic and abiotic factors at both small (*37*) and large scales (*14*, *15*, *34*). Here we show that O'ahu's novel networks notably resemble the structure and stability of native-dominated networks elsewhere. This high degree of similarity between novel and native-dominated networks suggests that the processes that structure interactions in such communities are largely independent of species identity and that ecological filtering occurs over relatively short (ecological) time, leading to functionally similar sets of players as compared with systems that have long evolutionary histories. Yet, because filtering depends on the pool of species introduced, novel networks may have an incomplete set of roles fulfilled. For example, in Hawai'i, large frugivorous birds are absent, resulting in a lack of dispersal of large native fruits (*38*). Therefore, functional characteristics (e.g., beak, seed, and fruit sizes) and species abundance (*39*) may be more important in the structure of mutualistic networks than species identity, supporting the role of ecological fitting (*40*). Thus, further investigation on the influence of functional traits and abundances on novel networks may shed light on the ultimate mechanisms driving network structure and species roles.

By studying novel networks across scales and comparing them with native-dominated networks worldwide, we identify several key considerations. First, sampling across scales is critical for testing generalizability of patterns and identifying the underlying processes (e.g., abiotic or biotic) structuring networks. Thus, explicitly examining multiple spatial scales is an essential next step toward advancing the understanding of processes that define specialization and shape ecological networks (*41*). We also predict that the patterns described here are more likely to be found in other isolated ecosystems, such as oceanic islands or isolated habitat patches, which are more prone to species invasions than less-isolated ecosystems. Second, our results show that introduced dispersers incompletely fulfill species roles lost by O'ahu's extreme scenario of plant and bird loss and introductions. Although these introduced birds on O'ahu are the only dispersers of native plants, they disperse a much higher proportion of seeds from invasive plants; therefore, their presence is a "double-edged sword" for conservation. The flexibility of birds and plants for partner switching and the fact that novel networks may be highly robust to species removal should be considered in restoration efforts. These efforts would benefit from initiatives that increase use of restoration sites by targeted frugivores and their consumption of native fruits. This would include outplanting commonly consumed native plants (e.g., *Pipturus albidus*) within plant restoration areas, removing commonly consumed introduced plants in sites with high densities of native fruits, and

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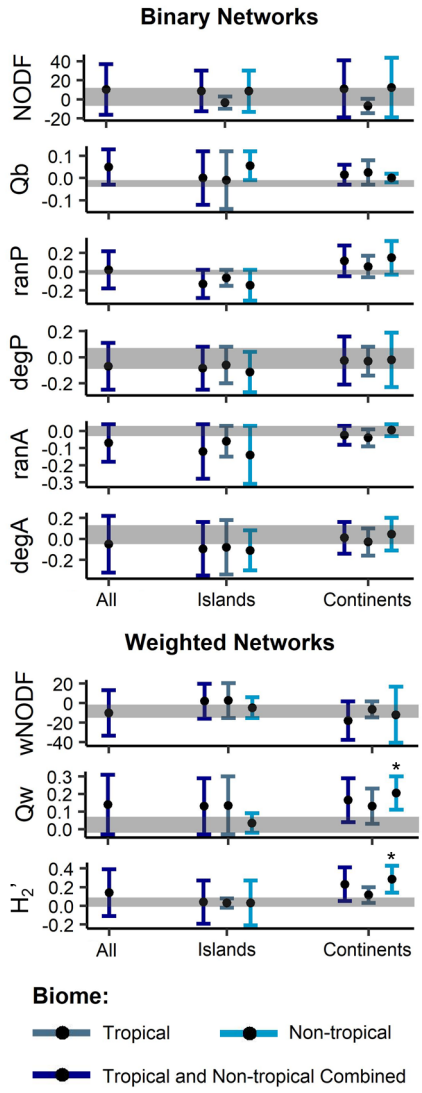

Fig. 4. Structure and stability of 42 SDNs from islands and continents in tropical and nontropical communities worldwide in comparison to novel networks on O'ahu. Significant difference (*) occurs when the 95% confidence interval of a metric for the seven sites in O'ahu (gray shaded area) does not overlap the intervals for non-O'ahu networks (colored bars). H_2', complementary specialization; wNODF and NODF, nestedness; Qw and Qb, modularity; ranP, ranA, degP, and degA, network robustness to the sequential extinction of animals (A) and plants (P) by random (ran) or from the most-generalist to the most-specialist species (deg). The latter is calculated only for binary data.

attracting (e.g., via playback) specific frugivores to restoration sites. The dramatic changes that have occurred in Hawaiian ecosystems provide an opportunity to better understand, anticipate, and mitigate the impacts of widespread and increasing biological invasions and species extinction, while also determining how network complexity develops.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S5
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Invasive birds spread native seeds

When humans introduce exotic species to sensitive ecosystems, invasion and extinction of native species often follow. The resulting ecological communities can develop unusual interactions between the survivors and newcomers. Vizentin-Bugoni *et al.* analyzed the structure of seed dispersal networks in Hawai'i, where native bird species have been mostly replaced by invaders. They found that the native plants now depend on the invasive birds for seed dispersal. The network of dispersal interactions is complex and stable, which are features of native seed-dispersal networks in other parts of the world. It appears that introduced species may, in some circumstances, become integrated into native ecosystems.

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