



Ecological correlates of species' roles in highly invaded seed dispersal networks

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Ecosystems with a mix of native and introduced species are increasing globally as extinction and introduction rates rise, resulting in novel species interactions. While species interactions are highly vulnerable to disturbance, little is known about the roles that introduced species play in novel interaction networks and what processes underlie such roles. Studying one of the most extreme cases of human-modified ecosystems, the island of O'ahu, Hawaii, we show that introduced species there shape the structure of seed dispersal networks to a greater extent than native species. Although both neutral and niche-based processes influenced network structure, niche-based processes played a larger role, despite theory predicting neutral processes to be predominantly important for islands. In fact, ecological correlates of species' roles (morphology, behavior, abundance) were largely similar to those in native-dominated networks. However, the most important ecological correlates varied with spatial scale and trophic level, highlighting the importance of examining these factors separately to unravel processes determining species contributions to network structure. Although introduced species integrate into interaction networks more deeply than previously thought, by examining the mechanistic basis of species' roles we can use traits to identify species that can be removed from (or added to) a system to improve crucial ecosystem functions, such as seed dispersal.

ecological restoration | Hawaii | mutualisms | novel ecosystems | plant-animal interactions

Increasing rates of extinction and invasion have led to the emergence of novel ecosystems around the globe (1–6). In such ecosystems, species without shared evolutionary histories often cooccur and interact, forming novel interaction networks (5–7). In these networks, introduced species may assume key roles, driving ecosystem structure and functioning, and thus changing ecological and evolutionary trajectories (3, 8). Previous studies have focused on low to moderately invaded systems (8, 9); however, in systems that have experienced severe invasions and widespread extinctions, examination of species' roles (species importance for network structure) and the mechanistic basis of these roles have rarely been investigated. Filling these knowledge gaps is critical for understanding the processes underlying the assembly of novel communities, and for predicting and mitigating the effects of species losses and invasions (3, 10).

Seed dispersal by animals is one of the most crucial ecosystem functions, linked to plant population dynamics, community structure, maintenance of biodiversity, and regeneration of degraded ecosystems (11, 12). A seed dispersal network (SDN) consists of mutualistic interactions between animal and plant species in a community, whereby animals benefit from consuming fruit and plants benefit by having their seeds moved away from parents (11). Previous studies of SDNs show that the role of a species is associated with specific characteristics, such as degree of frugivory (the proportion of a species' diet that consists of fruit) and social behavior for animals (13–15), and seed size and

fruit energetic content for plants (15). Although relative abundances, morphological, and behavioral characteristics often influence seed disperser–plant interactions, some variables that are widely known to influence mutualistic interactions have received little attention in the examination of species' roles (16–18; but see refs. 19–21). Furthermore, different mechanisms may operate at distinct spatial scales (22). Yet, if and how ecological correlates of species' roles are spatially consistent is not known. Identifying the mechanistic basis of species' roles across spatial scales is critical for predicting the types of species that can drastically alter networks. This, in turn, may have important applied implications because management measures may depend upon whether species interact randomly and establish interactions in proportion to their abundances and distributions (neutral processes) (23) and whether functional traits related to species' niches facilitate or constrain interactions (niche-based processes) (16, 18).

The Hawaiian Archipelago is arguably the world's capital of extinctions and invasions (5). In this system, crucial ecosystem functions associated with forest dynamics and structure, such as seed dispersal, have been profoundly modified (6, 24, 25). On

Significance

Species invasions and introductions are reshaping ecosystems around the world. In such novel ecological scenarios, it remains unclear whether crucial ecosystem functions played by lost native species may be partially or fully replaced by introduced species. We show that introduced plants and seed dispersers may take over interaction networks, playing key roles and governing network structure, with potential implications for its dynamics. The roles species play in novel networks are, however, defined by similar mechanisms that shape native-dominated communities. This indicates that the impacts of introduced species on invaded ecosystems can be anticipated based on ecological characteristics. Our results provide valuable recommendations for ecosystem management and restoration of increasingly degraded biological communities worldwide.

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O'ahu, all native frugivores are extinct, leaving seed dispersal almost entirely dependent on introduced birds (6). Here, we quantified the roles of native and introduced birds and plants in the novel SDNs of O'ahu. We also tested which morphological, behavioral, and demographic variables were associated with species' roles across spatial scales. Roles were defined based on a species' contribution to network structure using data from seven field sites. Our dataset encompasses interactions identified via analyses of 3,438 fecal samples from 24 bird species (*SI Appendix, Table S1*) and 4,897 d (~117,528 h) of camera trapping on 58 fruiting plant species (*SI Appendix, Table S2*), resulting in 18 bird species recorded dispersing seeds of 57 plant species. The data were used to build interaction matrices where each row represents a bird species i and each column represents a plant species j , with intersections, a_{ij} , representing either presence or intensity of interactions between pairs of species (*Materials and Methods*).

Results and Discussion

Introduced species numerically dominate SDNs on O'ahu; only 11.1% of bird species and 46.4% of plant species in the networks are native to O'ahu, 93.0% of all seed dispersal events are between introduced species, and no native species interact with each other (6) (updated data in *SI Appendix, Tables S1–S4*). These interactions provide a unique opportunity to understand variation in—and the ecological correlates of—species' roles in highly novel networks.

Introduced Species Shape Novel Networks. We found that introduced dispersers played more important roles in structuring network connectivity, nestedness, and modularity than the remaining native dispersers, while native and introduced plants only differed in structuring modularity. In particular, introduced dispersers contributed more to network structural stability (connectivity; in the sense of ref. 26) and functional redundancy (nestedness) than native dispersers, while both introduced plants and dispersers played most of the core roles that led to the existence of modules of highly connected species (modularity).

To examine connectivity, we calculated normalized degree (ND), which describes the proportion of available partners a species interacts with and is related to a species' importance for network cohesion and stability. For example, the loss of highly connected species more rapidly accelerates the rates of secondary extinctions in mutualistic networks compared to the loss of less connected species (27). We calculated ND for each disperser and plant species at the regional scale (all seven sites combined) and local scale (each site separately). For the regional network, introduced dispersers had higher NDs than natives and, while introduced plants showed the highest NDs, the difference between native and introduced plants was not significant (Fig. 1 and *SI Appendix, Fig. S1 and Tables S5 and S6*). These same trends were observed for local networks (Fig. 1 and *SI Appendix, Figs. S2 and S3 and Tables S7 and S8*). For the dispersers, the only two native bird species interacted exclusively with the introduced plant, *Clidemia hirta* and, therefore, contributed little to connectivity (Fig. 1A). This result is not surprising given they are not primarily frugivorous, and is in line with findings for less invaded communities where native birds tend to be more specialized than introduced birds (28). In contrast, native plants demonstrated some importance in the network, with certain native plants being as highly connected as introduced ones (e.g., *Clermontia kakeana* [acronym CLEKAK] and *Pipturus albidus* [acronym PIPALB in site Tantalus (TAN)]) (Fig. 1B).

We evaluated species' contribution to nestedness (29). Nestedness is the tendency of species with fewer partners (specialists) to interact with subsets of the partners of the more generalist species, which in turn also interact among themselves (30). A more nested network implies a more stable network because functional redundancy is high, resulting in the more generalist

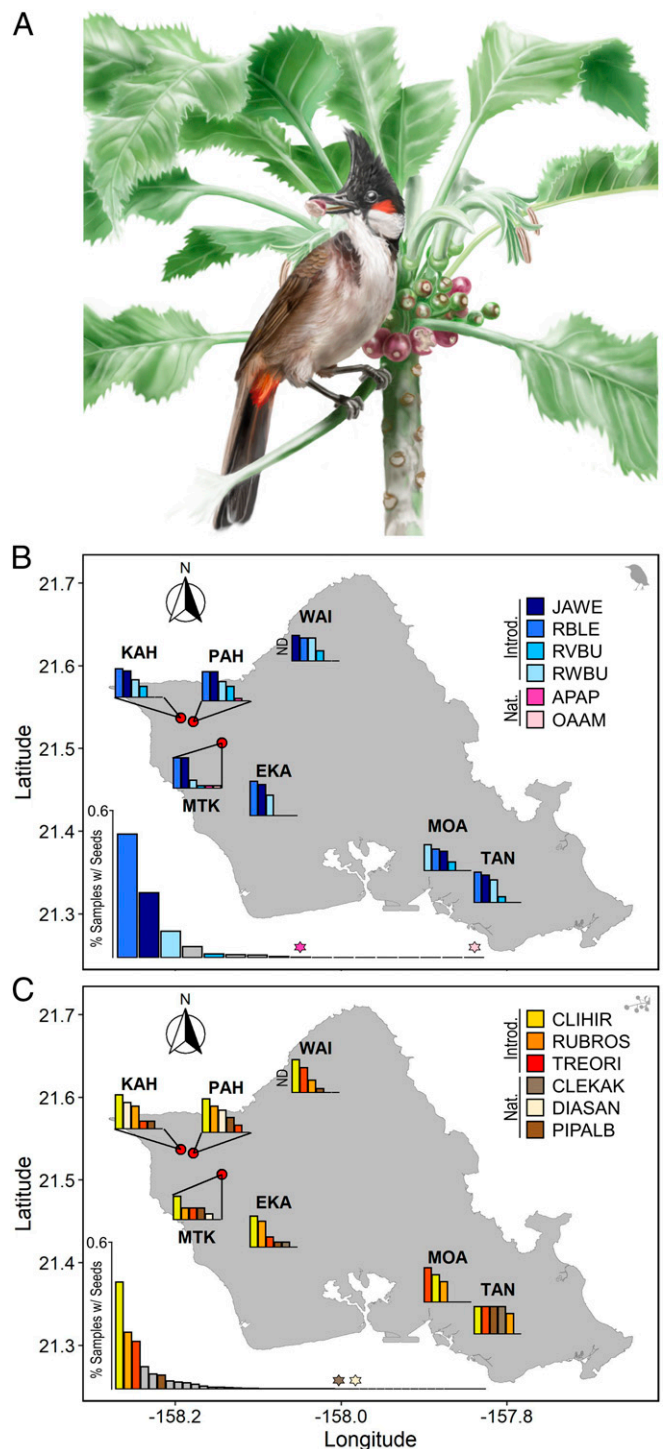


Fig. 1. The introduced *Pycnonotus jocosus* feeding on the endangered native *Delissea waianaensis* (A) and the seven smaller histograms showing normalized degrees of the most connected native and introduced disperser (B) and plant (C) species for the local SDNs on O'ahu. Larger histograms represent the proportion of all fecal samples with viable seeds for each disperser species (B) and the proportion of all fecal samples with viable seeds for each plant species (C). Stars indicate species with high ND whose bars are too small to see. For full species names, see *SI Appendix, Tables S1–S4*. Image credit in A: Pedro Lorenzo (artist).

species being capable of interacting with the partners of lost specialists (23, 31, 32). This analysis (and the one below) was performed only on the regional network, as local networks were

often small, potentially compromising the estimation of meaningful nestedness and modularity metrics (*Materials and Methods*). Similar to ND, introduced disperser species had a higher contribution to network nestedness than native dispersers, while introduced plants and native plants did not differ (*SI Appendix, Fig. S1 and Tables S5 and S6*). This result is in line with findings for a global dataset of pollination networks, where contribution to nestedness differed more for animals than for plants (33). Thus, introduced dispersers contributed more to increasing functional redundancy, which is expected to increase network stability (32), compared to native dispersers. Similarly, introduced dispersers have been reported to be more generalist species and compensate for native bird declines in New Zealand communities (28).

We used weighted networks (considering interaction intensities estimated based on fecal data) to evaluate species' contributions to the modular organization of interactions. Modularity occurs when subsets of species interact more among themselves than with other species, forming "modules" of highly connected species within the network (34). High modularity implies the existence of high niche partitioning caused by preferences (e.g., for high lipid fruit) or barriers (e.g., spatiotemporal and morphological matching) that constrain interactions to a subset of partners (18). In a modular network, species may differ in their contributions to within-module and among-module connectivity and, based on that, four possible roles can be recognized: Network hubs (high importance for within-module and among-modules connectivity), module hubs (more important for within than among-module connectivity), connectors (more important for among than within-module connectivity), and peripherals (low importance for both among and within-module connectivity) (*Materials and Methods*). We found that only introduced species were categorized as network hubs, including one disperser (*Leiothrix lutea*, acronym RBLE) and one plant (*Rivina humilis*, acronym RIVHUM) (Fig. 2). While no disperser acted as module hub, two introduced plants played such a role (*C. hirta*, acronym CLIHIR, and *Trema orientalis*, acronym TREORI). All dispersers acting as connectors between modules were introduced (two species). Similar numbers of introduced (26.7%; 8 of 30 species) and native plants (35.7%; 5 of 14 species) acted as connectors. The only two native dispersers and most native plants (64.3%; 9 of 14 native species) acted as peripherals (Fig. 2 and *SI Appendix, Tables S5 and S6*). Therefore, the modular structure of the SDN is primarily shaped by introduced dispersers and plants that are highly connected (network and/or module hubs) or bind distinct modules together (connectors), while native species play mostly secondary roles (peripherals). Previous work on pollination networks in native-dominated communities found most species act as peripherals and few species act as module and network hubs (35); here we found a similar pattern for SDNs in introduced-dominated communities.

Taken together, our findings indicate that even the most important native species play secondary roles for connectivity, nestedness, and modularity, thus reinforcing that introduced species now govern the structure and functioning of these novel SDNs. Because most remaining native species in these networks are poorly connected and play peripheral roles, their loss is expected to have fewer implications for network structure than the loss (or removal) of highly connected, introduced species (4, 27, 36).

Ecological Correlates of Species Roles. To understand the mechanistic underpinnings of species' roles, while accounting for species relatedness, we examined species characteristics known to influence bird–fruit interactions and the assembly of SDNs (13–15, 17, 19, 37). Specifically, we evaluated how attributes of the dispersers (abundance, degree of frugivory, range over the

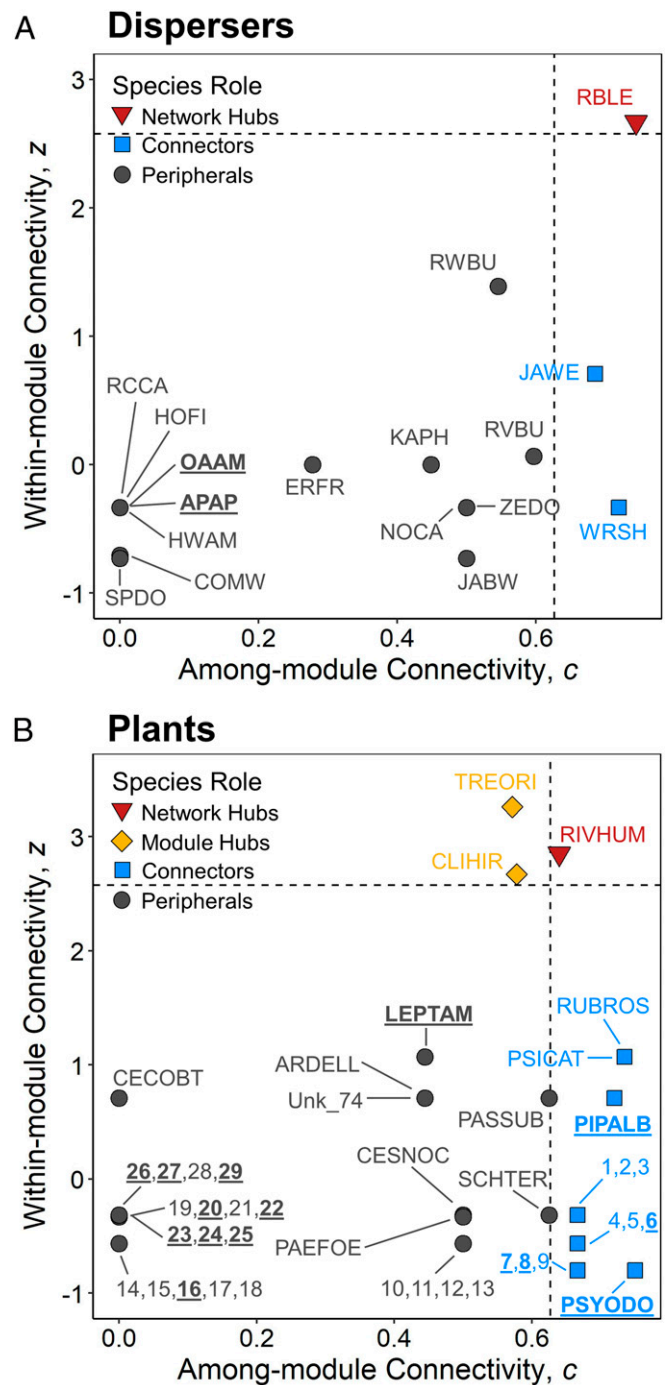


Fig. 2. Role of the 17 disperser (A) and 44 plant (B) species in the modular weighted island-wide SDN on O'ahu, Hawaii. Native species are in bold and underlined. Shorter lines within a plot stemming from one symbol show species that fell on the same position on the graph (i.e., similar z and c values). Dashed lines represent threshold values for c and z . For acronyms, and number codes for plants, see *SI Appendix, Tables S1–S3*.

island, and bill gape) (*SI Appendix, Tables S9–S18*) and attributes of the plants (abundance, range over the island, duration of fruiting, seed size, and proportion of carbohydrates, lipids, and proteins in the fruits) (*SI Appendix, Tables S19–S28*) influence species contribution to network nestedness, within-module connectivity, and among-module connectivity at the regional scale, and species connectivity (ND) at both spatial scales.

For dispersers, we found that species' roles were influenced primarily by degree of frugivory, followed by gape width, with results consistent across scales, and then by abundance and range, with results inconsistent across scales (Figs. 3A and 4A). At the regional scale, species importance in the network was positively associated with degree of frugivory (in three of four metrics), abundance (one metric), and range (one metric), and negatively associated with gape width (one metric) (Fig. 3A). At the local scale, ND increased with degree of frugivory and decreased with gape width, but was not associated with abundance and range (Fig. 4A). The magnitude of response (i.e., β -estimates) was greatest for degree of frugivory compared to the other predictors across both scales (Figs. 3A and 4A); thus, more frugivorous species disperse more plant species and have a greater influence on network structure. While the importance of degree of frugivory on species' roles supports findings from native-dominated communities (13–15; but see ref. 20), this work also highlights the importance of species abundances, which is a well-known driver of interaction frequencies in mutualistic networks (e.g., refs. 16–21 and 23), but has been less extensively studied with respect to its impact on species' roles (but see refs. 20 and 21). Studies in less invaded networks have reported inconsistent associations between the number of seed disperser partners and morphological traits (such as gape width and body mass) but consistent positive associations with range and abundance (21, 28). We found that species with smaller gape widths interacted with fewer partners at the local scale and were important for within-module connectivity at the regional scale, and species with larger ranges and higher abundances interacted with more partners only at the regional scale. These mixed results suggest that the importance of disperser distributions and abundances for connectivity may be scale-dependent. More investigations are necessary to determine whether the importance of these variables differ between native and novel communities.

For plants, we found that species' roles were associated with a combination of characteristics that often varied with spatial scale (Figs. 3B and 4B). At the regional scale, species importance in the network was positively associated with plant abundance (two of four metrics), proportion of lipids in fruits (one metric), and

range (one metric), and was negatively associated with seed size (one metric) (Fig. 3B). At the local scale, ND increased with duration of fruiting and proportion of lipids in fruits, and decreased with seed size (Fig. 4B). Overall, this indicates that plants with higher fruit availability (high abundance and broad range), smaller seeds, and higher lipids contributed more to network structure regionally; while duration of fruiting was only important locally, duration of fruiting and fruit and seed traits defined the number of dispersers a plant interacts with. While our results on the influence of fruit and seed traits are similar to native-dominated communities (15), our findings also demonstrate the relevance of fruit availability (fruiting duration, abundance, and range) on defining species influence on SDNs (15, 21, 37–39). In fact, although the influence of fruiting duration, abundance, and range on plants' connectivity to dispersers has been previously reported, their importance on species' roles has been inconsistent across different native-dominated communities (21). Further investigation is warranted before generalizations on the importance of these predictors in native and introduced-dominated communities can be made.

Ecological Correlates Vary Across Trophic Levels and Scales. Studies on native-dominated ecosystems have debated the relative importance of neutral and niche-based processes that drive mutualistic interactions (16, 18, 40). Neutral processes refer to random chance of encounters of partners, resulting in abundant and widespread species interacting with more partners, and more frequently, than rarer species (23). Alternatively, niche-based processes refer to morphological, physiological, and/or spatio-temporal matches (or mismatches) in species attributes or preferences that may constrain interactions (16). Although their relative importance may vary among communities, neutral and niche-based processes are not mutually exclusive and often both sets of processes are occurring (e.g., refs. 16–18, 21, 23, and 39–41).

For species-colonizing islands, interactions are predicted to be primarily driven by neutral processes (6) because of niche broadening and interaction release (9, 42). Contrary to this expectation and similar to native-dominated communities (13–16,

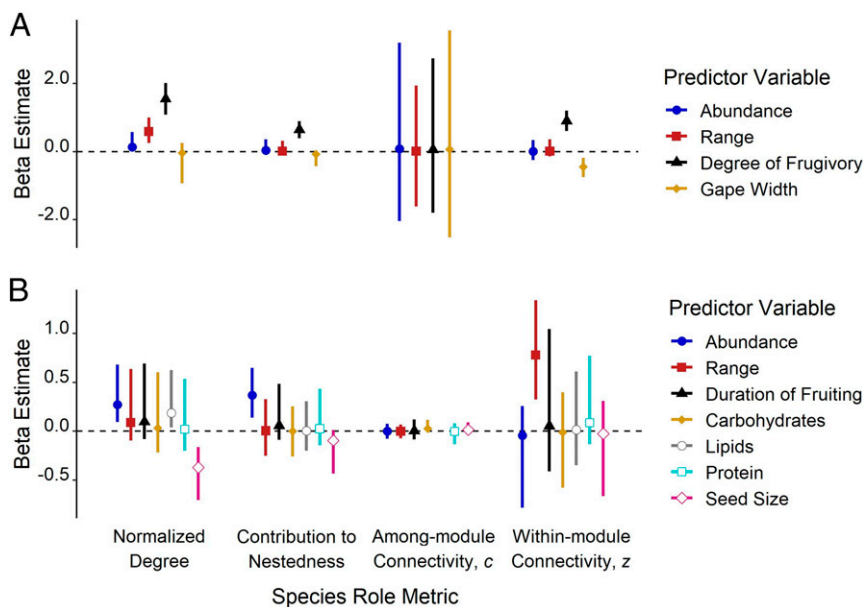


Fig. 3. Ecological correlates of the roles played by dispersers (A) and plants (B) in the regional SDN on O'ahu, Hawaii. β -Estimates show the direction and strength of the association between each of the predictor variables and the four complementary metrics of species' roles. A predictor was considered statistically significant when the 95% confidence interval did not cross zero. Output based on results from GLMMs accounting for species phylogenetic relationships. Degree of frugivory represents the proportion of a species' diet that consists of fruit.

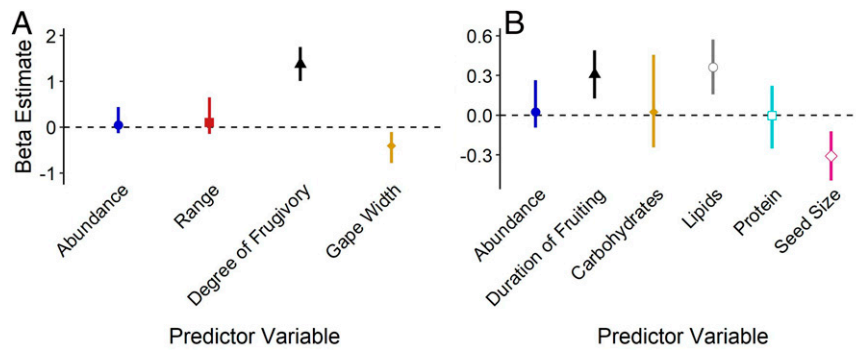


Fig. 4. Ecological correlates of the connectivity (ND) of dispersers (A) and plants (B) in the seven local SDNs on O'ahu, Hawaii. β -Estimates show the direction and strength of the association of normalized degree and each of the predictor variables. A predictor was considered statistically significant when the 95% confidence interval does not cross zero. Output is based on results from GLMMs accounting for species phylogenetic relationships.

21), we found that while both neutral (e.g., abundance, range) and niche-based processes (e.g., degree of frugivory, seed size) influenced SDNs, niche-based processes influenced species' roles across spatial scales and often had a stronger impact (larger β). Furthermore, disperser and plant characteristics associated with niche-based processes were largely similar to the ones in native-dominated communities (13–15, 21). This suggests that the mechanisms driving seed dispersal interactions may be similar in native-dominated and novel ecosystems (16, 17, 39), and ultimately may explain why the structure of the novel SDNs on O'ahu resembles those of native-dominated communities worldwide (6).

Both neutral and niche-based processes drove interactions for both trophic levels, but the importance of these processes was scale-dependent. In support of the neutral hypothesis, the number of plants a bird species dispersed (i.e., disperser's ND) was regulated by species abundance and range only at the regional scale, while niche-based processes (e.g., degree of frugivory and gape width) were important at both scales (Figs. 3A and 4A). Thus, disperser species that consumed more fruit and had larger gape widths dispersed more plant species, but the probability of encountering partners also impacted the number of plants dispersed regionally in the novel ecosystem. For plants at the regional scale, species importance depended on abundance, range, seed size, and lipids (Fig. 3B); thus, both the probability of being encountered by dispersers (neutral processes), as well as fruit and seed traits that constrain interactions (niche-based processes), influenced species' roles. In contrast, at the local scale, plant connectivity was primarily associated with niche-related traits, including nutritional content, seed size, and duration of fruiting (Fig. 4B). These results emphasize the need to analyze spatial scales separately to understand the interplay of neutral and niche-based processes on species interactions across trophic levels.

Implications for Conservation and Management. The key seed dispersers on O'ahu are all introduced species that largely disperse seeds of introduced plants which, in turn, become key players in the system. This suggests an “invasional meltdown” (43, 44), where positive feedback among introduced partners make them increasingly widespread and abundant, shaping the SDNs. Although introduced species often integrate into mutualistic networks (6, 33, 36, 45), no previous study has investigated their roles in highly altered communities. Our extensive multiscale dataset provides insights into the roles played by introduced (and the few remaining natives) species in novel SDNs, as well as the ecological correlates influencing them.

While lack of historical data prevents direct comparisons of the species' roles between the original (precolonization) and

current (novel) networks in Hawaii, evidence shows that gape width and body mass have significantly shifted downward following frugivore extinctions and introductions (46). These shifts have likely caused broad patterns of dispersal limitation in large-seeded plants (46), ultimately resulting in the secondary roles of large-seeded plants that we found here. Extinct large-bodied and large-gaped frugivores, such as corvids and terrestrial anatids, likely had core roles in the past SDNs consuming a large range in seed sizes and a large quantity of seeds (46). Similarly, we found here that introduced frugivores with larger gape widths consumed a greater number of plant species. Furthermore, the only two native birds still present are small-bodied passerines with small gapes and which predominantly feed on items other than fruits; thus their roles are likely to have always been minimal.

Our findings have important implications for management. First, the analysis of species' roles may provide guidance for targeted management of plant communities. For example, management may include the removal of highly connected introduced plants (e.g., *C. hirta* and *T. orientalis*), but also out-planting of highly connected native plants (e.g., *P. albidus* and *C. kakeana*). In fact, in sites with active management, some native plant species had connectivity levels as high as introduced plants (i.e., Fig. 1, site TAN), indicating restoration can increase the contribution of native species to SDN structures. Nevertheless, introduced plants remained highly connected in all sites, indicating that removal of introduced plants is also needed to reduce their importance. Furthermore, targeting the disperser species that are highly frugivorous and can be enticed to consume native fruits (e.g., Japanese white-eye, acronym JAWE) would be another effective management strategy (47). Second, by knowing the ecological correlates of species' roles in SDNs, managers can target species possessing traits linked to high importance for network structure and stability. For example, native plants that have long fruiting durations, small seeds, and fruits rich in lipids are more likely to be dispersed and, therefore, have greater potential for self-sustaining populations. Similarly, introduced species possessing these traits should be targeted and controlled in the early stages of invasion, before they become fully integrated into the network. Thus, even though we show that introduced species can integrate into SDNs more deeply than previously thought, their importance for network structure can be anticipated based on ecological characteristics. This has great value for ecosystem management and restoration of increasingly degraded biological communities worldwide. To advance our understanding (and generalizations) on the predictability of species' contributions to network structure based on their ecological characteristics, we urge more studies across communities with distinct levels of invasions and extinctions, particularly analyzing trophic levels and spatial scales separately.

Materials and Methods

Study Site. This study took place on O'ahu, which is the most populated and the most human-modified major island in the Hawaiian Archipelago. We collected data from seven sites that encompass the regional variation in mean annual rainfall (from 1107.8 mm to 3386.1 mm), elevation (108 to 1206 m above sealevel), and invasion (introduced species comprise 71.4 to 100% of the bird species, and 47.1 to 100% of the plant species present in the networks) (6) (*SI Appendix, Table S4*). The seven sites were 'Ekahanui (EKA), Kahanahāiki (KAH), Moanalua (MOA), Mount Ka'ala (MTK), Pahole (PAH), Tantalus (TAN), and Waimea Valley (WAI). Some of these sites (EKA, KAH, MTK, PAH, and TAN) receive active management, which includes removal of introduced plants, rodent control, and outplanting of native species, which is done in small patches (i.e., less than half hectare).

Sampling Interactions. We recorded interactions primarily based on the identification of seeds on fecal samples and secondarily based on motion-activated cameras for plant species not detected in fecal samples. For fecal sampling, we caught passerine birds using mist-netting from November 2014 to December 2017 (6). For game birds, feces were collected from February 2017 to December 2018 in the three sites where the two main species (*Lophura leucomelanos* and *Pternistis erckelii*) are common (EKA, KAH, and PAH). For game birds, samples were collected from individuals caught using traps or collected from the ground and subsequently identified using DNA barcoding of the ITS2 region, with sequences compared to those in GenBank. For fecal samples collected from the ground, we discarded the part in contact with the soil to remove material deposited on the ground that adhered to the sample. All three methods were implemented within the same area for each site. In total, we processed 3,438 fecal samples collected from 24 bird species. We considered an interaction only when the seed found in the fecal samples was unbroken (no cracks) and, therefore, was probably viable (necessary for seed dispersal).

To increase interaction detection, we used data from motion-activated cameras. We prioritized monitoring rare native (and a few introduced) species (*SI Appendix, Table S1*), which make them harder to detect in fecal samples. These plants were not detected in fecal samples, except for five species (*SI Appendix, Tables S29*). Most of these species have relatively specialized traits (i.e., large ornithocorous fruits and large seeds), and prolonged fruiting seasons, which increase the probability of engaging in rare interactions that are harder to detect (48). Cameras were installed in front of plants with ripe fruits to obtain footage and later reviewed manually, summing up to 4,897 d (approximately 117,528 h) of camera trapping on 58 plants with ripe fruits (*SI Appendix, Table S2*). As with data from the fecal samples, an interaction was counted only when the bird-plant interaction likely resulted in seed dispersal. This occurred when the bird swallowed the whole fruit or pieces of fruits if seeds were small, and when the plant species had hard-coated seeds that come out intact from birds' gut, even in species with strong gizzards (e.g., game birds).

First, we produced one regional (island-wide) and seven local (one per site) binary interaction networks (based on presence or absence of an interaction) using data from game cameras and fecal samples. Thus, if a plant was ever found being consumed on camera or found in a fecal sample of a bird species, it was considered a 1, otherwise, a 0. We produced binary networks here because the two distinct sampling methods (i.e., cameras and fecal) limit the ability to create comparable interaction intensities. However, combining these methods provides an inclusive and robust estimate of whether the fruit of a particular plant species was consumed by a particular bird. Specifically, adding game camera data increased the number of links detected by 24.7% (42 of 170 links were only detected on cameras). These networks were used for analyses of connectivity (ND) and nestedness, which are both binary metrics, at both scales (see *Species' Roles*, below).

Second, we produced a weighted network (considering interaction frequencies) based only on fecal samples for the regional scale, which was used for the analysis of modularity (see *Species' Roles*, below). Although most studies describing species' roles use binary datasets and metrics designed for binary networks (e.g., refs. 14, 20, and 21), we calculated a weighted network because interaction frequencies provide more accurate descriptions of the impact of one species on another in mutualistic networks (49). As in Vzentin-Bugoni et al. (6), interaction frequencies a_{ij} were calculated as the proportion of samples of a given bird i that presented intact seeds of the plant species j . We only used fecal sample data because interaction frequencies cannot be derived in a comparable way from distinct sources of data (i.e., feces and cameras). We did not produce a separate weighted network based on game camera data

because that method was only used to complement interaction detection on rarer species; therefore, game camera data alone underestimate the diversity of species and interactions of the community. Because interactions from camera data were only included in the binary networks, these matrices encompass more species than the weighted networks (based only on fecal data) (*SI Appendix, Table S4*). We did not produce weighted networks for the local scale because of the poor performance of weighted species-level metrics, such as c and z (see *Species' Roles*, below), for small size networks (e.g., 6 to 10 bird species in our case) (*SI Appendix, Table S4*).

Species-Specific Variables.

Disperser abundances. The number of individuals seen or heard was estimated at 6 to 13 points in each site. In every site except EKA, the point count locations were along trails central to the site and at least 150 m apart. In EKA, the point counts were laid out in a 150-m grid. In every site, each point was located in such a way that each point had woody vegetation at least 2 m tall within 40 m from the point. All sites were visited every 7 wk, and point counts were conducted between dawn (~30 min before sunrise) and 6 h later. Surveys were not conducted in heavy rain or high winds (>7 on the Beaufort scale). The surveys followed a 2-min period of silence and lasted 8 min. Every bird recorded was identified and had the distance from the observer estimated. After the survey, the intensity of rain (none, light, moderate), cloud cover (percent of visible sky obscured by clouds), and wind speed (Beaufort scale) were recorded. If gusts were observed during the counts, the average between the strengths of the sustained wind and gusts was used.

Only birds detected within 40 m of the point were used to model the abundance of each species per site, taking into account changes in detectability due to weather conditions, time of survey, and the month of the survey. By using only birds detected within 40 m, changes in detectability due to distance from the observer were negligible. A zero-inflated Poisson mixed model was conducted for each species. To account for sites where a species was not detected because it was outside its distribution, the zero-inflated part of the models were intercept-only models, with site as a random effect. The count part of the models included observer category (14 total) and site as random effects and variables that may influenced detectability (intensity of rain, cloud cover, wind speed, time since sunrise, and month) were treated as fixed effects. All models were run using the *glmmTMB* function in the R-package *glmmTMB* package (50). We then compared models of all combinations of the fixed effects using the *dredge* function in the *MuMIn* package (51). The model with the lowest Akaike's Information Criterion corrected for small sample size (AICc) was then selected (hereafter referred to as the "detection model") and used in subsequent analyses to estimate abundance.

To include the effects of the various habitats on bird abundance across all points, we used the top ranked detection model (above) for each bird species and then added the standardized (mean centering and dividing by the SD) point-level and site-level habitat variables. The point-level habitat variables included average canopy height, average canopy cover, and elevation, and the site-level habitat variables included plant-species richness, proportion of fleshy-fruited plant species, and proportion of introduced plant species. We also included the square of elevation. Using the *dredge* function, we ran models for all combination of habitat variables, while keeping the variables from the detection model in all models, and then averaged the models that accounted for 95% of the cumulative model weight using the function *model.avg* in the R-package *MuMIn* package (51). Using the average habitat model for each species, we estimated the abundance of each bird species at each point, averaged over the year. These estimates were then averaged for each site. See Gleditsch (52) for more detail in the estimation of bird species abundances. Permits for this study were University of New Hampshire Institutional Animal Care and Use Committee nos. 140502, 150601, 151003, and 160204.

Disperser morphology. For each bird caught using mist-nets (passerine birds) or traps (gamebirds) from January 2015 to December 2018, we measured bill gape and weight. We then used the average across all individuals for both variables, excluding all juveniles and recaptures (*SI Appendix, Table S5*).

Range. Disperser's range on O'ahu was estimated as the number of sites a species was recorded at least once over the study period. Presence in one site was defined based on mist netting, game camera, and point count data.

Degree of frugivory. Degree of frugivory was a measure of the dependence of a disperser species on fruits. Based on the fecal dataset for all seven sites combined, we calculated the proportion of samples for each species in which

intact seeds were found. If a sample had multiple seed species, they were counted independently. This is based on the assumption that species that feed infrequently on fruits will rarely have seeds in their feces and, therefore, have a low degree of frugivory.

Fruit abundances. Fruit abundances were estimated using seed rain traps placed in each site: 100 traps in MOA, WAI, and EKA; 150 traps in MTK and PAH; 148 traps in KAH; and 146 traps in TAN. Traps were placed 10 m apart, except in TAN where they were 5 m apart. Each trap had a diameter of 0.243 m and an area of 0.046 m² and was covered with chicken wire to deter animals from removing seeds and fruits. Once a month, the cotton cloth at the bottom of the traps was collected, dried, and the seeds were identified under a stereomicroscope. To obtain local abundances, we started by dividing the number of seeds of each species in each trap by the average number of seeds per fruit (estimated from fruits collected in the field) to obtain the number of fruits per trap. We then summed the number of fruits per species across all traps at the site and, finally, calculated the relative abundances (i.e., dividing the number of fruits found for each species in a given site by the total number of fruits across all species in that specific site). To obtain the regional abundances we averaged the total number of fruits produced across all sites and then calculated the relative abundances.

Duration of fruiting. We defined duration of fruiting as the number of months a species produced fruits over the year, which was compiled from multiple sources of data. We conducted phenology surveys in each site. These surveys included monitoring 10 individuals per species (or all individuals if fewer than 10 were available) every 7 wk from June 2015 to December 2016. We complemented this dataset using data on seeds found in fecal samples, seed traps, and game cameras (see *Sampling Interactions*, above).

Seed morphology. Fruits of most species ($n = 39$) were collected at our field sites and had at least 10 seeds measured to estimate the average seed width. For missing species, measures were taken from seeds found on feces or from photos taken with scales in our reference collection (14 species) or from photos with scales retrieved from online images from museums or published articles (3 species).

Nutritional content. Fresh fruits were collected in the field and had their pulp removed in the laboratory. From the pulp, we quantified the proportion of dry mass corresponding to proteins, carbohydrates (water-soluble carbohydrate), and lipids. The minimum quantities used for each species were 207 mg for lipid, 81 mg for carbohydrates, and 41 mg for protein analyses (details in ref. 53).

Plant range. Plant range was estimated as the number of sites at which species was recorded producing fruits over the study period.

Species' Roles. Species' roles were quantified using widely used complementary metrics (13, 15), which we calculated for both dispersers and plants. For regional and local scales, we calculated species ND that describes the proportion of the available partners a species interacts with and is often correlated to other metrics related to how connected and central a species is in a network (54). For the regional network, which is known to be both significantly nested and modular (6), we also calculated per species contribution to such topologies. Specifically, we calculated the per species contribution to nestedness which, for a species i , is the difference between the observed nestedness and the nestedness obtained when only interactions of the species i are randomized according to a null model. As described in Saavedra et al. (29), nestedness was quantified using the NODF metric, which calculates the nonoverlapping and decreasing fill of the interaction matrix (30), and a null model for which the probability of a cell to be filled (i.e., receive an interaction) depends on the degree (i.e., number of partners) of the animal (columns) and the plant (rows) (12). For this, we used the function *nestedcontribution* in R-package *bi-partite* (55). We also quantified species roles for modularity. First, we calculated the modularity metric Q using the DIRTLPAwb+ algorithm, which searches for the maximum modularity possible (34). As this is an optimization algorithm, the maximum modularity may vary among runs so we repeated this five times and accepted the highest Q -value obtained Q (0.27). We then calculated for each species i , the within-module connectivity (z):

$$z_i = \frac{k_{is} - \bar{k}_s}{SD_{k_s}}$$

where k_{is} is the number of links a species has within its module s , and \bar{k}_s and SD_{k_s} are the average and SD of the number of links across all species within

the module s , respectively; and we also calculated for each species i , among-modules connectivity (c):

$$c_i = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2,$$

where k_i is the number of links (i.e., degree) of species i , k_{it} is the degree of species i across all modules t , including its own module. If all interactions of i are restricted to its own module, then $c_i = 0$; if i has the same number of links with each module $c_i = 1$ (56).

We used the same thresholds given in terms of SD units away from the mean of a normal distribution as Guimerà and Nunes Amaral (56) and Olesen et al. (35) (i.e., $c = 0.62$ and $z = 2.57$) to classify species into four roles: Network hubs (high c and z), module hubs (low c , high z), connectors (high c , low z), and peripherals (low c and z).

Analyses. We used generalized linear mixed models (GLMM) to test whether ND, contribution to nestedness, within-module connectivity (z), and among-module connectivity (c), all response variables, were related to species-specific variables, the predictors. For dispersers, predictors were relative abundances, degree of frugivory, range, gape width, and body mass; and for plants, predictors were relative abundances, range, duration of fruiting, seed width, and proportion of proteins, lipids, and carbohydrates. Analyses followed general recommendations by Zuur et al. (57). All predictor variables were scaled by mean centering and dividing by the SD prior to analysis to make beta parameter estimates comparable. We used Pearson correlations to test for multicollinearity ($r \geq 0.70$), which resulted in the exclusion of disperser body mass (*SI Appendix, Table S4*), but no variable was excluded a priori for plants ($r < 0.70$) (*SI Appendix, Table S5*). Model fitting was performed using the *glmmTMB* function in the R-package *glmmTMB* package (50) using β , γ , or Gaussian distributions, depending on the response variable. To account for phylogenetic nonindependence among closely related species, all models had a random effect representing "family" for birds and "order" for plants. Bird taxonomy was obtained online from <http://birdtree.org>, which follows Jetz et al. (58) classification. Plant taxonomy was compiled using the *taxize* R-package (59), which uses the Integrated Taxonomic Information System (<http://itis.gov>). For the local scale, we added "site identity" as a random effect in the GLMMs because some species occurred in multiple sites. We then used the function *dredge* of the R-package *MuMIn* (51) to compare models including all possible combinations of predictor variables, plus an intercept-only model. We performed model selection based on the AICc. Finally, as there was not a single model with >90% of the model weight (60), we conducted model averaging. To avoid model overparameterization and convergence issues, we had to remove one predictor variable from two of the models. We removed the least-influential predictor variable (one where removal had the smallest impact on AICc), which included "range" from the plants' ND model (Fig. 3B) and "lipids" in the plants' c model (Fig. 4B).

Data Availability. All study data are included in the article and supporting information.

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