Multiscale analysis of canopy arthropod diversity in a volcanically fragmented landscape

Elske K. Tielens [ID],[1,†] Maile N. Neel,[1] Devin R. Leopold [ID],[2] Christian P. Giardina,[3] and Daniel S. Gruner [ID][1]

[1]*Department of Entomology, University of Maryland, College Park, Maryland, USA*
[2]*Department of Botany and Plant Pathology, Oregon State University, Oregon, USA*
[3]*Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, Hawai'i 96720 USA*

Abstract.   Habitat fragmentation resulting in habitat loss and increased isolation is a dominant driver of global species declines. Habitat isolation and connectivity vary across scales, and understanding how connectivity affects biodiversity can be challenging because the relevant scale depends on the taxa involved. A multiscale analysis can provide insight in biodiversity patterns across spatial scale when information on dispersal ability is not available, in particular for community-level studies focusing on multiple taxa. In this study, we examine the relationship between arthropod diversity, patch area, and connectivity using a multiscale approach. We make use of a natural experiment on Hawai'i Island, where historic volcanic activity has transformed contiguous native forests to lava matrix and discrete forest patches. This landscape of patches has persisted for 150 yr, and we selected 10,000 ha consisting of 863 patches to analyze landscape connectivity using a graph theory approach. We collected arthropod samples from *Metrosideros polymorpha* tree canopies in 34 forest patches during multiple years. We analyzed the relationship of arthropod diversity with area, as well as with connectivity across increasing scales, or dispersal threshold distances. In contrast to well-established ecological theory as well as prior work on birds and fungi in this system, we did not find support for a canonical species–area relationship. Next, we calculated connectivity across spatial scales and found lower Shannon diversity with higher connectivity at small scales, but no effect at increased dispersal threshold distances. We examined the landscape structure and found all habitat patches connected into three subnetworks at a 350 m threshold distance. All patches were connected at 700 m threshold distance, indicating structural dispersal limitation only at small scales. Our findings suggest that canopy arthropods are not dispersal limited at scales shown to impact both soil fungi and birds in this system. Instead, Hawaiian canopy arthropods may perceive the landscape as a connected area where discrete forest patches and the early-successional matrix contribute resources that vary spatially with regard to habitat quality. We argue for the utility of multiscale approaches, and the importance of examining maintenance of biodiversity in fragmented landscapes that persist for hundreds of years.

Key words: biodiversity; canopy arthropods; connectivity; fragmented landscapes; graph theory; Hawai'i; *Metrosideros polymorpha*; patch isolation; spatial scale; species–area relationship.

† **E-mail:** elske.tielens@gmail.com

INTRODUCTION

Change in land use is a leading driver of declining biodiversity worldwide, and most species now occur in fragmented landscapes of degraded habitat (Pereira et al. 2010, Haddad et al. 2015). Fragmented landscapes are widespread; for example, 70% of all forests globally

are within 1 km of a forest edge, and nearly 20% are within 100 m of an edge (Haddad et al. 2015). Habitat fragmentation generally occurs in conjunction with habitat loss, and it has been difficult to quantify the contribution of loss of area relative to changes in spatial configuration of patches, patch shape, and isolation. Reductions in area result in a decline in biodiversity, for example, because smaller patches have fewer resources, smaller populations, and lower genetic diversity and likely attract fewer new colonizing species (Simberloff and Wilson 1969, Simberloff 1976, Gibb and Hochuli 2002, Steffan-Dewenter et al. 2002). While negative effects of habitat loss on biodiversity are widely supported (Curtis 1956, Preston 1962, Watling and Donnelly 2006, Didham et al. 2012), the effects of fragmentation independent of area are less clear (Tscharntke et al. 2002, Haddad et al. 2017a, b). Habitat fragmentation was long considered unimportant in comparison with the effects of loss of area (Fahrig 2003), but recent reviews on this subject have reopened this question and led to vigorous debate (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019). Researchers disagree on appropriate definitions, whether studies should take place at landscape or patch scale, and how fragmentation should be quantified, and consensus has not yet emerged (Tscharntke et al. 2002, Fahrig 2003, 2017, Haddad et al. 2017a, b, Fletcher et al. 2018, Fahrig et al. 2019).

Habitat fragmentation can affect diversity by reducing landscape connectivity, or the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993). A decrease in landscape connectivity can reduce movement between patches (Collinge 2000), increasing extinction rates (Rybicki and Hanski 2013), reducing recolonization rates (Simberloff and Wilson 1969, Berggren et al. 2001), and decreasing species persistence (Ferraz et al. 2003, Orrock and Watling 2010). However, the prevalence and magnitude of these effects depends on the spatial scale in question as well as species' characteristics (Tischendorf and Fahrig 2000).

Alongside the landscape's physical attributes, including structural connectivity, functional connectivity of the landscape depends on the behavioral response of organisms to the landscape structure. Discrete habitat patches may still be connected for species that disperse over the intervening distances, whereas species that operate on smaller scales and disperse below interpatch distances will be isolated in individual patches. Thus, life history and behavioral characteristics, such as species movement ability, foraging patterns, and seed dispersal syndromes, influence the spatial scale at which a species interacts with the landscape (Henle et al. 2004, Umetsu et al. 2008, Jones et al. 2015). Despite its importance, dispersal ability is often an unknown parameter that is difficult to measure directly for many species. In such cases, community patterns can be examined by analyzing connectivity as a function of increasing spatial scale.

Graph theory approaches are well suited to such multiscale analyses because they allow integrated interpretation of patch-, class-, and landscape-level connectivity across an array of potential dispersal distances (Keitt et al. 1997, Tischendorf and Fahrig 2000, Calabrese and Fagan 2004). While recent debate on the effects of fragmentation on biodiversity focuses strongly on the relative value of patch- vs. landscape-scale studies (Fahrig 2017, Fletcher et al. 2018, Fahrig et al. 2019), multiscale graph theory allows for specifically incorporating the contribution of spatial scale in comparing connectivity between habitat fragments. Graph theory approaches connectivity by creating a spatially explicit depiction of the landscape (the graph) with individual patches existing as nodes and edges among them representing possible movement (Keitt et al. 1997). Metrics are calculated that summarize spatial relationships among nodes and allow overall landscape connectivity and the contribution of particular nodes to be quantified. Graph theory metrics can incorporate proximity, number and size of neighbors, and their centrality to the bigger network across a defined set of threshold distances. These variables can provide information on the role of connectivity in maintaining biodiversity, given the differences in scale across which organisms may operate.

Here, we present a multiscale graph analysis of habitat connectivity and biodiversity, combining landscape-scale remote sensing data with local sampling of arthropod communities. We utilize a patchy landscape of mature forest and primary successional volcanic substrate on Hawai'i Island, where historic volcanic activity

and two resulting lava flows in 1852 and 1881 have created a model fragmentation system of natural replicate forest patches, called kīpuka, that vary widely in size, shape, and isolation. The acute effects of this historic disturbance event have long since stabilized, and we can examine the role of area and connectivity among kīpuka independent of the habitat loss process. In particular, using a historically fragmented system allows us to avoid erroneous conclusions due to delayed effects of fragmentation on biodiversity over time and extinction debt (Tilman et al. 1994, Ewers and Didham 2006, Fletcher et al. 2018). The relatively homogeneous matrix surrounding kīpuka eliminates the need to incorporate the well-known effects of differential landscape resistance (Ricketts 2001, Kennedy et al. 2010) into our analyses. Prior work in the kīpuka landscape has demonstrated a canonical log–log species–area relationship for forest birds (Flaspohler et al. 2010), as well as correlations between kīpuka area, connectivity, and soil fungal diversity and composition (Vannette et al. 2016). However, we examine the effects of connectivity and area on canopy arthropods because these have very different life histories from the previously discussed taxa, including variation in dispersal ability, such as winged and unwinged species. We examine the role of area as well as connectivity between kīpuka in this model fragmentation study system to address the following questions with regard to canopy arthropods: (1) Does arthropod species richness increase with habitat kīpuka area? (2) How does the importance of connectivity and kīpuka area as predictors of arthropod diversity vary across spatial scale? (3) How does connectivity among discrete forest patches vary across spatial scale?

Materials and Methods

Study site

The study landscape was located on the northeast flank of Mauna Loa in the Upper Waiakea Forest Reserve on Hawai'i Island (19°38–41′ N, 155°20–23′ W). Two historic lava flows (c. 1852 and 1881) converted relatively continuous native wet forest dominated by *Metrosideros polymorpha* Gaudich. (Myrtaceae) into a series of remnant patches (Fig. 1; Wolfe and Morris 1996). The forest remnants left intact (termed kīpuka) are separated by a matrix consisting of 'a'ā and pāhoehoe basalt substrates (Harris et al. 2017). The matrix, in early primary succession, differs strongly from the 3000- to 5000-yr-old kīpuka forest with respect to microclimate and soil and vegetation composition (Carson and Clague 1995, Vandergast and Gillespie 2004) and is relatively consistent across the landscape. Matrix vegetation is predominately <2 m in height and characterized by shrubs such as *Vaccinium reticulatum* Sm. (Ericaceae), *Leptecophylla tameiameiae* Cham. & Schltdl. (Ericaceae), and scattered small-statured *M. polymorpha* trees. The native kīpuka forest is dominated in the overstory by *M. polymorpha* with a subcanopy of, among others, *Cibotium glaucum* Sm. (Cibotiaceae) and *Cheirodendron trigynum* Gaudich. (Araliaceae; Gruner 2004a, Flaspohler et al. 2010).

We chose a 10,000-ha landscape for our analyses and used kīpuka boundaries determined by Vaughn et al. (2014). We selected focal kīpuka across the landscape to span the variation in size (0.1–10.2 ha) and relative isolation (Fig. 1). We chose focal *M. polymorpha* trees that represented the modal size and forest canopy tree architecture. Within each kīpuka, we chose the representative canopy tree nearest the GPS point of the kīpuka centroid. For all kīpuka larger than 0.2 ha ($n = 24$), we selected a second tree by following a random compass bearing to within 10 m of the kīpuka edge and choosing the closest representative canopy tree. For each focal tree, we recorded tree height to the nearest meter using a clinometer and tape measure.

Arthropod sampling details

We sampled arthropods from the canopies of focal *Metrosideros polymorpha* trees within the kīpuka. In 2009, we sampled from interior ($n = 32$) and edge ($n = 24$) trees in 32 kīpuka. In 2010, we selected a subset of the previously sampled kīpuka, ensuring subset spanned both the range of kīpuka area and the full spatial extent of the study region. The 2010 kīpuka were sampled from both interior ($n = 16$) and edge ($n = 10$) trees. There was no difference in mean area between kīpuka that were included vs. excluded in 2010 ($\text{mean}_{overall} = 1.88$, $\text{mean}_{included} = 2.23$, $\text{mean}_{excluded} = 1.19$, $t = 1.143$, $P > 0.1$).

Arthropods were collected by branch clipping and bagging samples from focal trees from July to August each year, following the methods in
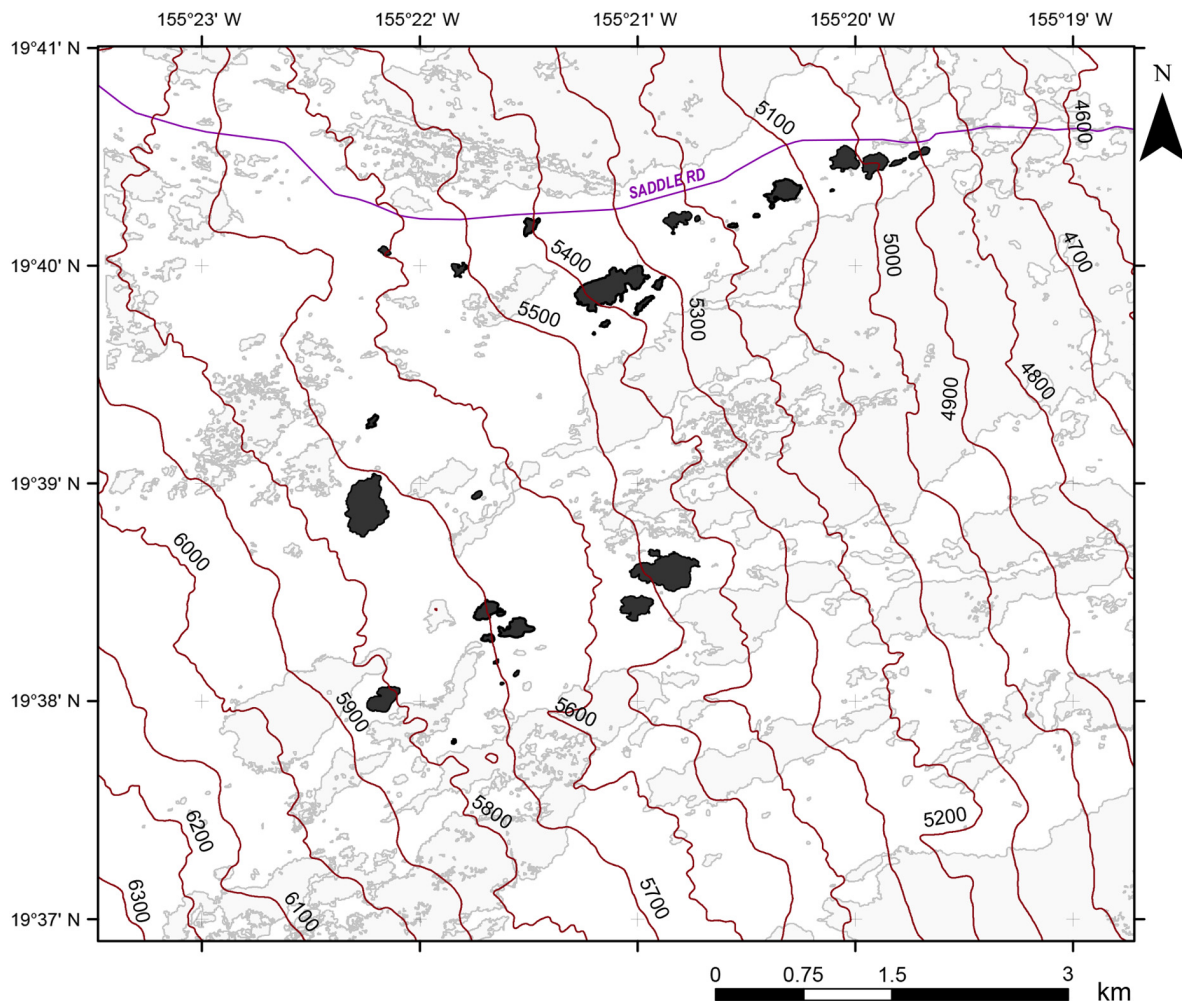
Fig. 1. Topographic map of the kīpuka landscape with forest fragments in gray, matrix in white, and forest fragments where arthropods were sampled in black. Elevation bands are included and labeled in feet. Map boundaries based on LiDAR remote sensing methods (Vaughn et al. 2014).

Gruner (2004). We took composite samples consisting of 4–6 upper-canopy terminal branches, containing ~0.25 m³ of foliage, for each focal tree. We sampled branches with a custom pole-pruner and net to catch clipped branches. When necessary, we accessed the canopy using the single-rope climbing technique (Perry 1978). All branch clips were collected directly into doubled 13-gallon, white polyethylene trash bags, which were sealed and stored in a shaded location to prevent arthropod escape and limit mortality before transport to the USDA Forest Service's Institute of Pacific Island Forestry in Hilo, HI, for processing on the same day of collection.

Arthropods were extracted from each sample by shaking portions of foliage over a table lined with a white sheet and collecting dislodged arthropods in vials filled with 70% ethanol. We repeated this process until all foliage and the collection bag were thoroughly searched. To quantify sampling intensity across samples, we recorded the total dry mass of separated leaves and stems after drying to constant mass at 70°C. Arthropods were sorted, counted, and identified to taxonomic species or morphospecies. A full list of collected arthropods can be found in Appendix S2. We measured specimen body length with an ocular micrometer to the nearest

millimeter size class. We then estimated biomass using taxon-specific regression equations developed from species in this study system (Gruner 2003).

Diversity and species–area relationship

We examined the relationship of diversity to kīpuka area for the 34 sampled kīpuka. We assessed arthropod diversity using three measures of Hill or effective species numbers (Hill 1973, Jost 2006): estimated asymptotic species richness using the nonparametric function ChaoRichness(), estimated asymptotic Shannon index using function ChaoShannon(), and estimated asymptotic Simpson index using function ChaoSimpson() (Chao et al. 2014), in the package iNEXT in R (Hsieh et al. 2016). These measures estimate the species richness curve asymptote as a measure of richness to compare across incompletely sampled assemblages (Chao et al. 2014). Species rarefaction curves were assessed before proceeding with extrapolated diversity values (Appendix S1: Fig. S1). We converted these diversity metrics to effective species numbers (Hill numbers for $q = 0$, $q = 1$ and $q = 2$). We assessed Pielou's evenness by dividing raw Shannon diversity by species number, using package vegan in R (Oksanen et al. 2018). We also estimated species density as the species count per unit plant mass, defined as load (Root 1973). We tested the hypothesis that area was correlated with various diversity indices and species density using linear mixed models with a fixed effect for kīpuka identity and an offset for foliage mass, and using log likelihood ratio tests, using package lmer. We compared species composition between edge and center trees using a PERMANOVA in the package vegan in R.

Graph theory

We used ArcGIS 10.1 to project the GIS layer of the 10,000-ha kīpuka landscape into PCS Universal Transverse Mercator Zone 5 to calculate patch area and select all kīpuka larger than 0.01 ha containing mature native forest as nodes (ESRI 2012). Pairwise distances among nodes were calculated from spherical weighted centroids using the Conefor Inputs extension for ArcGIS (Saura and Torné 2009). We calculated graph theoretic metrics (described below and in Table 1) at threshold distances at 50-m increments from 50 to 5500 m to provide a comprehensive description of the landscape and of each node. Nodes were considered connected by edges when they were within a chosen threshold distance. These edges signify ecological flux or potential dispersal of organisms between patches (Urban and Keitt 2001), and we considered all habitat patches within a subnetwork of nodes connected by edges (together known as a component) available to organisms capable of dispersing that distance. We specifically looked for threshold distances at which the metric changed dramatically, indicating the landscape was rapidly shifting from unconnected to connected coincident with varying dispersal capacity. All landscape-level metrics were quantified across the range of threshold distances mentioned above using the command line version of Conefor Sensinode V.2.6 (Saura and Torné 2009). We used custom Perl scripts to generate the commands for each Conefor run and custom R scripts to process the resulting data files.

First, we quantified the number of subnetworks in the landscape (number of components, NC) and connections among nodes (number of links, NL). To provide comprehensive connectivity measures, we used habitat availability (reachability) metrics based on the integral index of connectivity (IIC; Pascual-Hortal and Saura 2006, Saura and Rubio 2010). Integral index of connectivity describes landscape connectivity by weighing patch area and number of links between all pairs of patches in a landscape for a given dispersal distance (Pascual-Hortal and Saura 2006, Neel et al. 2014). It increases monotonically with area and proximity across the entire fragmentation gradient and thus is easy to interpret. Because it is a binary metric (the landscape is either connected or not connected at a given distance), it emphasizes threshold distances at which network connectivity changes dramatically (Pascual-Hortal and Saura 2006, Saura and Rubio 2010, Neel et al. 2014). We chose IIC because metrics that include area within a threshold distance are more accurate at estimating movement (Moilanen and Nieminen 2002, Bender et al. 2003) and immigration (Bender et al. 2003) of animals between patches than purely distance-based metrics such as nearest-neighbor distances. We used EC(IIC), a formulation of IIC that gives the area of one continuous patch that would

Table 1. Connectivity metrics used to analyze the kīpuka landscape as a whole and connectivity values for individual patches.

Type	Metric	Abbreviation	Definition	Literature
Landscape	Number of edges	NL	Total number of edges (i.e., connections between patches) in the landscape	
	Number of components	NC	Total number of components (i.e., subnetworks) in the landscape	
	Integral index of connectivity	IIC	The possibility of dispersal between different pairs of patches, as a function of patch area and overall landscape size. Quantifies the possibility that two points in the landscape are connected—because they are either in the same patch or in different patches that are connected. Dispersal is binary; that is, patches are either connected or not. The numerator of the equation calculating IIC measures habitat amount and possibility of connection, without taking into account overall landscape area.	Pascual-Hortal and Saura (2006)
	Equivalent connected area of integral index of connectivity	EC(IIC)	The area of a single patch of habitat that would yield the same IIC value as is seen in the observed landscape	Pascual-Hortal and Saura (2006)
	Change in integral index of connectivity	dIIC	The sum of IIC across all patches when one patch is removed. Quantifies how much connectivity is prone to decrease if changes in the landscape occur	Pascual-Hortal and Saura (2006)
Node	Change in number of edges	dNL	Change in number of edges in the landscape when patch k is removed	
	Change in number of components	dNC	Change in number of components in the landscape when patch k is removed	
	Change in integral index of connectivity	dIIC	Change in integral index of connectivity, that is, change in overall habitat reachability in the landscape when patch k is removChange in integral index of connectivity, that is, change in overall habitat reachability in the landscape when patch k is removed	Pascual-Hortal and Saura (2006)
	Intra portion of change in integral index of connectivity	dIICintra	Contribution of habitat area within a patch to the change in integral index of connectivity when patch k is removed	Bodin and Saura (2010), Saura and Rubio (2010)
	Connector portion of change in integral index of connectivity	dIICconnector	Contribution of the degree to which a patch connects other patches to the change in integral index of connectivity. Calculated based on the area of patches connected and the number of links needed to connect them	Bodin and Saura (2010), Saura and Rubio (2010)
	Flux portion of change in integral index of connectivity	dIICflux	Flux contribution to the change in integral index of connectivity. Calculates the connectivity for pairs of patches where the focal patch is either a source or destination	Bodin and Saura (2010), Saura and Rubio (2010)

yield the same value of IIC as the observed, fragmented IIC (Pascual-Hortal and Saura 2006).

To examine individual node importance for overall landscape connectivity, we calculated the percentage change in the value of NC, NL, and IIC before and after removal of each node (denoted as dNC, dNL, and dIIC). The larger the percentage change from the full network when a node is removed, the greater the contribution of that node to overall network connectivity. Integral index of connectivity is of particular interest because it also takes into account the existence of alternative paths when evaluating the effect of patch removal. Further, IIC can be partitioned into three independent portions: IICintra, representing the contribution of habitat within a patch; IICflux, the portion of connectivity for pairs of patches where the focal patch is a potential source or destination; and IICconnector, quantifying the degree to which a patch connects other patches, or functions as stepping-stone in the landscape (Bodin and Saura 2010, Saura and Rubio 2010, Neel et al. 2014). IICconnector is based on the area of the patches being connected

and number of links needed to connect them but is independent of focal patch area. This metric is sensitive to landscape configuration and the location of the patch in the larger landscape. Because these dIIC metrics are additive, the sum of values across all patches gives insight into the sensitivity to losses of patches and thus quantifies how robust or fragile the network is in terms of different aspects of connectivity. The three dIIC metrics provide a comprehensive and non-redundant view of the changes in different aspects of patch contributions to connectivity patches as measured by the consequence of their loss.

Relating arthropod communities to graph networks

To examine the relationship between our predictors and arthropod diversity, abundance, and species density, we modeled diversity measures using mixed-effect models and a model-averaging approach. We used generalized linear mixed models with Shannon diversity, abundance and species density as response variables and connectivity and area as fixed effects, kīpuka identifier as random effect, and log foliage mass as offset for sampling effort. We included the following predictors: kīpuka area, sampled tree height, change in number of components (dNC), change in the flux portion of integral index of connectivity (dIICflux), and change in the connector portion of integral index of connectivity (dIICconnector). We included tree height to explore the possibility that hyperlocalized area—approximated by focal tree maximum height—is a more relevant measure of habitat size. Tree height has previously been shown to be linearly related to canopy volume in kīpuka (Flaspohler et al. 2010). Correlation coefficients for connectivity metrics included in the model analysis were ≤0.3. We used the same predictors for mixed models explaining species density but excluded the offset.

All explanatory variables were centered and standardized to z values before use in models. We used the function dredge in the R package MuMIn to come to the best model (Bartoń 2018), and for global models without a model of clear best fit ($\Delta AIC_c > 4$), we used model averaging. We calculated variable estimates, confidence intervals (CIs), and relative importance for the averaged model

using the package lmer (Appendix S1; Bates et al. 2015). Coefficient of determination was based on corrected R^2 using the function r.squaredGLMM in package lmerTest.

RESULTS

Arthropod community description

We sampled 21,365 individuals for this analysis, across four different classes (Arachnida, Insecta, Diplopoda, and Malacostraca), 15 orders, and 106 species and morphospecies. Species richness in samples ranged from 11 to 33 species, with median richness of 22 species. Overall mean species richness was slightly higher in samples collected in 2010 than in 2009 (<1 standard deviation), but per kīpuka richness was similar. Pielou's evenness across samples was high with a mean of 0.84 for samples taken in 2009 and 0.87 for samples from 2010. Kīpuka edge and interior trees did not differ with respect to arthropod community composition (PERMANOVA pseudo-$F = 0.9727$, $P > 0.05$).

Species–area relationship

Kīpuka Shannon diversity did not correlate with kīpuka habitat area (Hill $q = 1$; likelihood ratio: $\chi^2 = 1.8919$, estimate = 0.2246, 2.5% CI = −0.09745, 97.5% CI = 0.2661, $P > 0.01$; Fig. 2). Other diversity measures showed similar patterns (effective species richness and Simpson diversity; Appendix S1: Table S1). In contrast to Shannon diversity, species density did slightly increase with kīpuka area (likelihood ratio: $\chi^2 = 6.7003$, estimate = 0.1573, 2.5% CI 0.04394, 97.5% 0.2661, $P < 0.05$; Appendix S1: Fig. S2).

Arthropod richness, abundance, and biomass across spatial scales

Significant predictors of arthropod diversity and abundance varied across spatial scales (Fig. 3, Tables 2, 3). Although connectivity in the landscape increased with dispersal threshold until 750 m, the subset of kīpuka where we sampled arthropods were connected in a single component at 350 m. As a result, connectivity metrics for sampled kīpuka did not vary above 350 m threshold distance and are not included here.

With increasing dispersal threshold, the importance of connectivity as explanatory variable for Shannon diversity decreased (Fig. 3, Table 2).
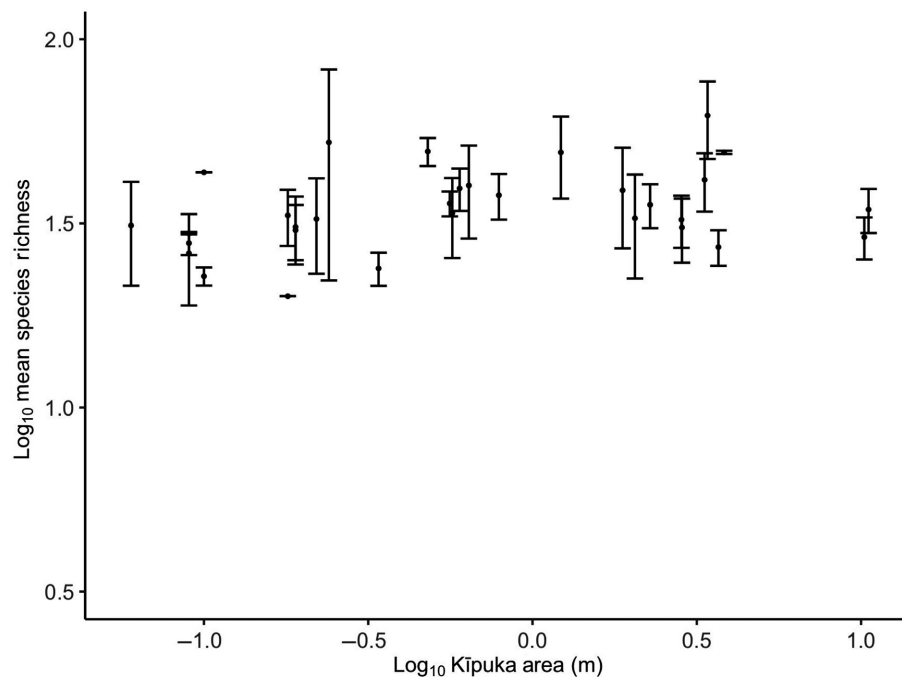
Fig. 2. $\log_{10}$ mean species richness as a function of $\log_{10}$ kīpuka area (m). Mean kīpuka species richness is based on center and edge trees sampled in 2009 and 2010. Error bars indicate standard error of the mean.

While dIICflux was negatively correlated with Shannon diversity at 50 m dispersal thresholds, above 50 m this relationship no longer occurred (Fig. 3). Partitioning dIIC into intra, connector, and flux portions indicated that this relationship primarily results from changes in dIICflux, which quantifies the role of a patch as source or destination and weighs patch area as well as the number of edges between them (Table 1, Fig. 3). Besides dIICflux, the averaged model explaining Shannon index at 50 m included sampling year as significant predictor (year, 0.4289 ± 0.1471, $P < 0.05$; dIICflux -0.2886 ± 0.1445, $P < 0.05$; Table 2). Above 50 m threshold distance, only sampling year was a significant predictor (at 100 m, year 0.4190 ± 0.1484, $P < 0.01$; at 150 m, year 0.4267 ± 0.1477, $P < 0.01$; at 200 m, year 0.4279 ± 0.1490, $P < 0.01$; at 250 m, year 0.4191 ± 0.1482, $P < 0.01$; at 300 m, year 0.4190 ± 0.1482, $P < 0.01$; Fig. 3, Table 2).

Landscape graph description

The landscape consisted of 863 kīpuka in 10,000 ha. The kīpuka size distribution ranged from 0.01 to 1011 ha, and median kīpuka size

was 0.07 ha. The distribution of pairwise distances between kīpuka was relatively uniform as a result of the high patch number in the landscape. Interpatch distances range from 9.90 to 12,172 m with a median of 4982 m.

At 350 m dispersal threshold, the landscape consisted of three components (i.e., three subnetworks in which all nodes are connected to at least one other node; Fig. 4). At dispersal threshold distances ≥350 m dispersal distance, the graph was highly interconnected with many redundant paths connecting nodes, suggesting decreasing importance of any single node for overall connectivity. At a threshold of 700 m, the landscape was connected in a single component. Number of links among kīpuka increased linearly with threshold distance (Fig. 4). EC(IIC), which represents the size of a single contiguous patch that would have a given IIC value, increased with threshold distance, indicating increasing habitat availability (Fig. 4). When the landscape was completely disconnected, EC(IIC) was 1301.19 ha, increasing to 2086.96 ha at the lowest threshold at which all patches were united in one component (700 m). Maximum EC
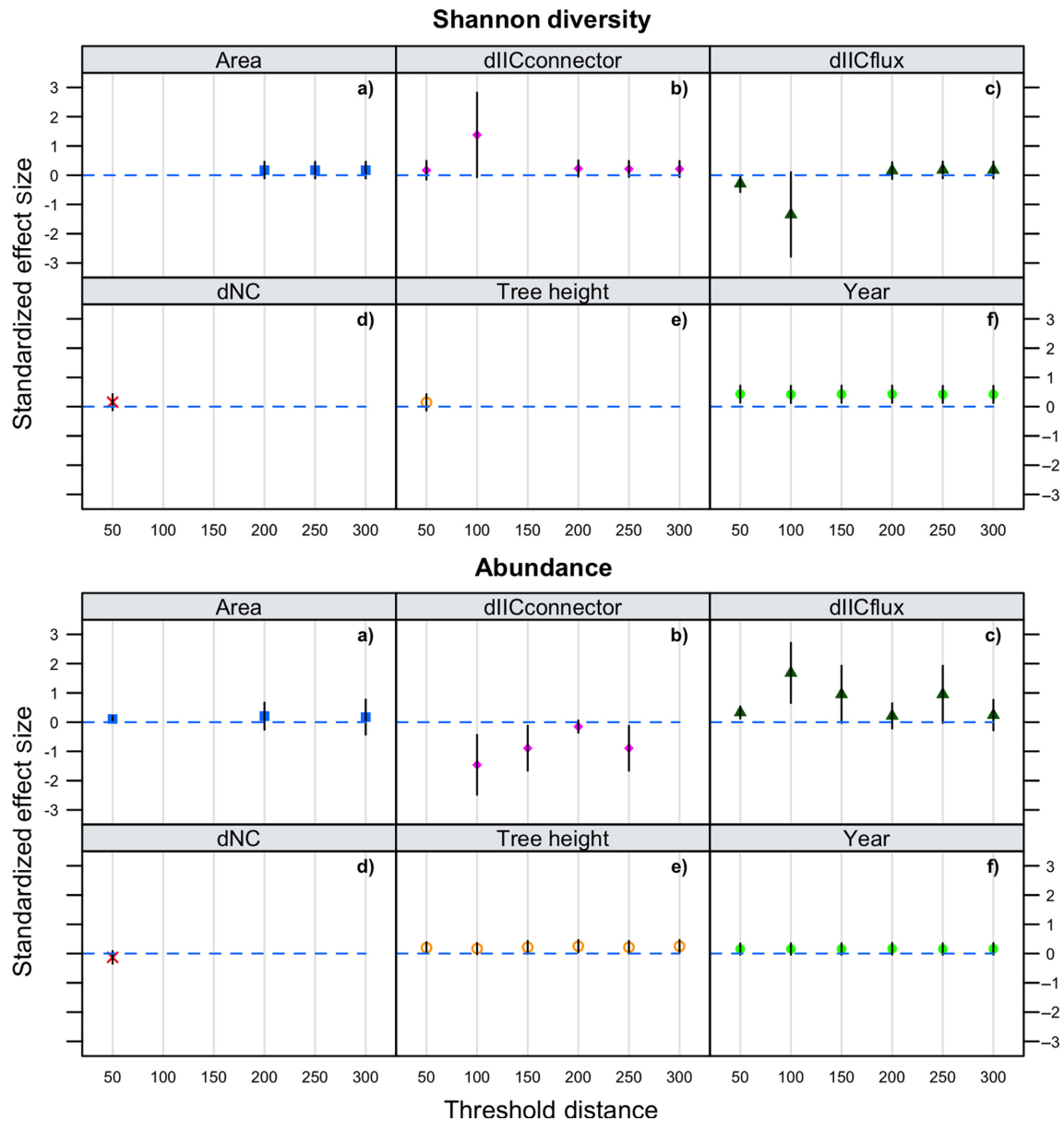
Fig. 3. Effect sizes for the relationship between connectivity and Shannon diversity (top) and abundance (bottom) across threshold distances. Effect sizes are standardized to z values (mean and variance) of data. Panels show (a) area, (b) connector portion of integral index of connectivity after patch removal, (c) flux portion of integral index of connectivity after patch removal, (d) change in number of components, (e) tree height, and (f) year.

(IIC) was found at 5500 m when all kīpuka were directly connected to one another. With increasing threshold distance, dispersal limitation was reduced, resulting in a decrease in dIICintra while an increasing proportion of connectivity was contributed by movement among kīpuka: dIICflux. dIICconnector peaked when distance was below 350 m, and then decreased as the number of redundant pathways among kīpuka increased, and consequently, the importance of individual kīpuka as stepping-stones decreased (Fig. 4).

Table 2. Model coefficients of response variables included in averaged model explaining effective estimated Shannon diversity (Hill 1).

| Distance | Shannon diversity | | | | | |
	Year	Area	Tree height	dIICconnector	dIICflux	dNC
50	0.4289 ± 0.1471**	–	0.1463 ± 0.1416	0.1681 ± 0.1620	−0.2886 ± 0.1445*	0.1550 ± 0.1388
100	0.4159 ± 0.1514**	–	–	1.376 ± 0.7250	−1.343 ± 0.7239	–
150	0.4267 ± 0.1477**	–	–	–	–	–
200	0.4279 ± 0.1490**	0.1745 ± 0.1438	–	0.2289 ± 0.1391	0.1570 ± 0.1452	–
250	0.4191 ± 0.1482**	0.1745 ± 0.1438	–	0.2138 ± 0.1380	0.1802 ± 0.1440	–
300	0.4190 ± 0.1482**	0.1745 ± 0.1438	–	0.2115 ± 0.1441	0.1774 ± 0.1441	–

Notes: Values represent averaged standardized model estimates and standard errors (unitless). We used linear mixed-effect models, averaging all models for which $\Delta AIC_c < 4$. Variables not included in best models are indicated by en dashes. Estimates, standard errors, confidence intervals, and importance of the variable in the averaged model can be found in Appendix S1.
*$P < 0.05$; **$P < 0.01$.

Table 3. Model coefficients of response variables included in averaged model explaining arthropod abundance.

| Distance | Arthropod abundance | | | | | |
	Year	Area	Tree height	dIICconnector	dIICflux	dNC
50	0.1543 ± 0.09861	0.1082 ± 0.0476*	0.1999 ± 0.0975*	–	0.3287 ± 0.1044**	–
100	0.1554 ± 0.09914	–	0.1699 ± 0.0985	−1.458 ± 0.5144**	1.685 ± 0.5175**	–
150	0.1544 ± 0.09959	–	0.2160 ± 0.1117	−0.8906 ± 0.3854*	0.9502 ± 0.4646	–
200	0.1652 ± 0.1015	0.2072 ± 0.2329	0.2520 ± 0.1076*	−0.1517 ± 0.1064	0.2157 ± 0.2169	–
250	0.1544 ± 0.09959	–	0.2160 ± 0.1117	−0.8906 ± 0.3854*	0.9502 ± 0.4946	–
300	0.1611 ± 0.1016	0.1723 ± 0.3026	0.2513 ± 0.1088	–	0.2417 ± 0.2621	–

Notes: Values represent averaged standardized model estimates and standard errors (unitless). We used linear mixed-effect models, averaging all models for which $\Delta AIC_c < 4$. Variables not included in best models are indicated by en dashes. Estimates, standard errors, confidence intervals, and importance of the variable in the averaged model can be found in Appendix S1.
*$P < 0.05$; **$P < 0.01$.

DISCUSSION

Although the species–area relationship is often regarded as a general law in ecology (McGuinness 1984, Rosenzweig 1995, Drakare et al. 2006) and has been supported for other taxa in the kīpuka landscape (Vandergast and Gillespie 2004, Vandergast et al. 2004, Flaspohler et al. 2010, Mueller 2015, Vannette et al. 2016), we did not find a correlation between canopy arthropod richness and kīpuka area. Furthermore, patch connectivity did not correlate strongly with observed diversity. Lastly, we found that small expansions in dispersal threshold rapidly increase landscape connectivity. Together, these results suggest that the kīpuka landscape is both structurally and functionally connected for canopy arthropods. This landscape-level diversity pattern results from three interacting variables: the nature of the matrix, Hawaiian canopy arthropod dispersal ability, and structural connectivity in the kīpuka landscape.

One explanation for the lack of species–area relationship is that the matrix may not serve as a barrier to dispersal. The kīpuka and the matrix differ both in structure and in microhabitat (Vandergast and Gillespie 2004, Flaspohler et al. 2010), but small-statured *M. polymorpha* (shrubs < 3 m) occur across the matrix. Functional connectivity is higher in landscapes where vegetation structure or microclimate is similar for the matrix and the habitat (Ricketts 2001, Prevedello and Vieira 2010, Eycott et al. 2012, Öckinger et al. 2012). Second, matrix landscapes often act as sinks or even sources of organisms (Haynes et al. 2007, Schmidt et al. 2008, Umetsu et al. 2008). *M. polymorpha* trees occurring in the matrix supported higher abundances of arthropods than trees in the kīpuka, but with strong differences in community composition (unpublished data). We conclude that canopy arthropods do differentiate between the two habitats, but we hypothesize that contrary to other kīpuka-dwelling taxa and our assumptions (Flaspohler et al. 2010, Mueller
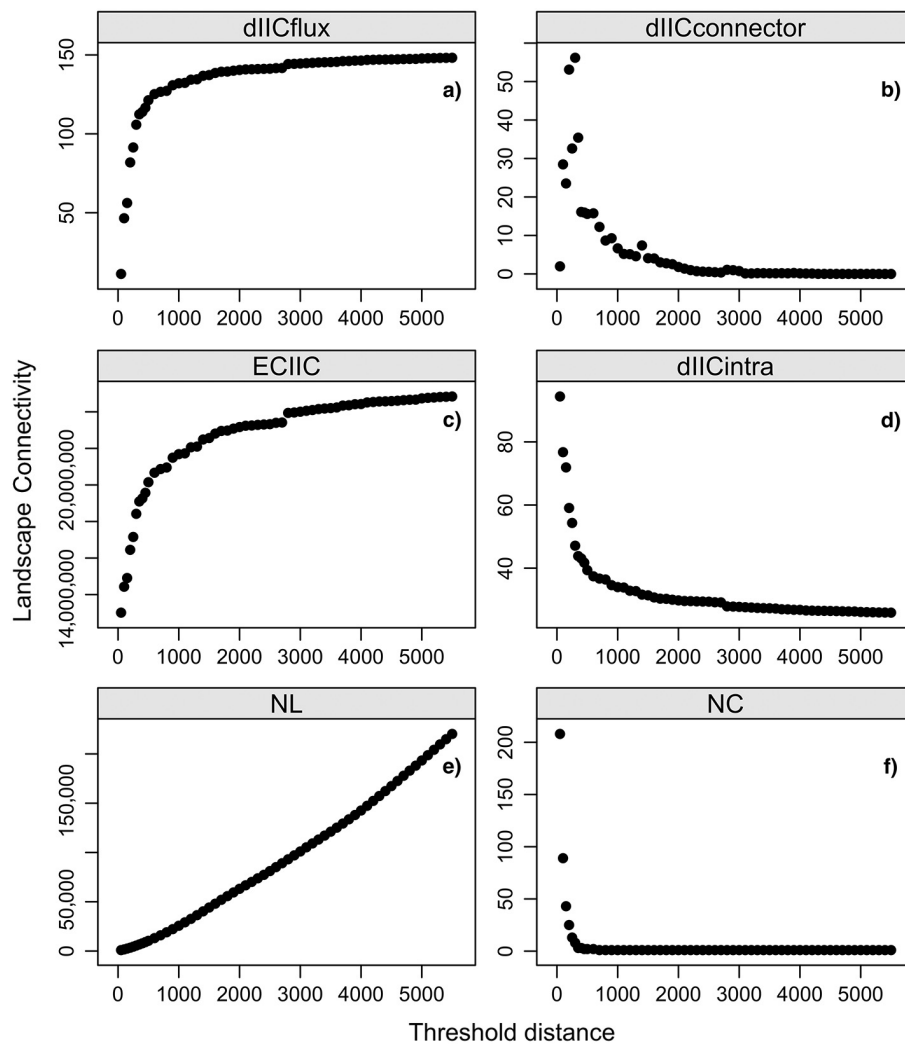
Fig. 4. Landscape connectivity as a function of dispersal threshold. Panels show (a) change in flux portion of the integral index of connectivity, (b) change in connector portion of the integral index of connectivity, (c) change in equivalent area of the integral index of connectivity, or the amount of connected habitat necessary to provide the same amount of connectivity as a given IIC, (d) change in intra portion of the integral index of connectivity, (e) change in number of links in the landscape, and (f) change in number of components in the landscape.

2015, Vannette et al. 2016, Knowlton et al. 2017), canopy arthropods do not experience the matrix as strongly hostile. Although we cannot determine conclusively without measuring dispersal, our results suggest that the matrix is permeable and there is a high degree of movement across the landscape.

Dispersal ability and life history characteristics determine how organisms perceive and interact with landscape patchiness and may explain differences in species–area relationship between our work and many other studies in fragmented landscapes (Rosenzweig 1995, Holt et al. 1999, Cagnolo et al. 2009, Phillips et al. 2017), including other taxa in the same kīpuka system. For example, species richness increases with area for root fungi associated with *M. polymorpha* (Vannette et al. 2016), for *Drosophila* flies (Mueller 2015), and for birds, particularly non-native species (Flaspohler et al. 2010). Additionally, gene flow is limited between understory *Tetragnatha* spider populations in the kīpuka (Vandergast

and Gillespie 2004, Vandergast et al. 2004). Also, fungal communities (Vannette et al. 2016) and understory spiders (Vandergast and Gillespie 2004, Vandergast et al. 2004) in more connected patches are more similar to one another in species composition, indicating possible dispersal limitation. However, these taxa may have very different habitat use from canopy arthropods. Fungi may be dispersal-limited, particularly those with specialist resource or habitat requirements (Norros et al. 2012, Nielsen et al. 2016), and while *Drosophila* are active flyers, they do not make use of *M. polymorpha* (Mueller 2015) and may perceive the matrix to be more impermeable. Bird species, on the other hand, are highly dispersive (Knowlton et al. 2017) and select kīpuka for foraging, and will be sensitive to differences in conditions between kīpuka and the matrix. Our study combines a highly patchy landscape with taxa that are likely moderate dispersers, for which the matrix may be more permeable due to the ability of canopy arthropods associated with *M. polymorpha* to make short-term use of the matrix. For canopy arthropods, we found no evidence for variation in the species–area relationship across dispersal strategies or body size (Appendix S1: Table S2). This contrasts with expectations based on theory (Holt et al. 1999, Tscharntke and Brandl 2004, Jones et al. 2015, van Noordwijk et al. 2015) as well as prior findings in kīpuka fungal communities (Vannette et al. 2016). It is possible that canopy arthropods are sufficiently dispersive due to their relatively small size. For many Hawaiian canopy arthropods, wind is hypothesized to be the main mode of dispersal (Howarth 1987, 1990), and as a result, body size and dispersal ability do not affect their mobility between kīpuka.

The large number of patches and short distances among kīpuka result in a landscape that is structurally connected at small spatial scales. Connectivity among the kīpuka increases rapidly with threshold distance, as the number of components in the landscape decreases. The slope of the equivalent connected area of the integral index of connectivity is steep at low dispersal thresholds. At threshold distances larger than 350 m, the sampled kīpuka are all connected in a single network component. At this threshold distance, the network has many redundant connections, so individual kīpuka contribute little to overall landscape connectivity. Partitioning the integral index of connectivity supported this, where the dIIC portion quantifying the importance of nodes as stepping-stones connecting other nodes, dIICconnector, peaked at 350 m before rapidly declining, while connectivity provided by area within a node, dIICintra, decreased consistently with increasing dispersal threshold. Canopy arthropod diversity and abundance only correlates with connectivity for threshold distances ≤100 m. We conclude that the kīpuka landscape is functionally well connected for canopy arthropods, as dispersal in similar taxa commonly exceeds those distances (Hanski 1994, Denno et al. 1996, Eber 2004).

For canopy arthropods, the kīpuka landscape may be best understood as a heterogeneous landscape of varying resource quality, rather than a series of disconnected fragments. Variation in arthropod diversity across kīpuka can be driven by differences in arthropod abundances as a result of resource availability or quality. Specifically, canopy arthropod communities are directly (for primary consumers) or indirectly (for higher trophic levels) dependent on tree or canopy size. Tree height roughly corresponds to canopy volume (Flaspohler et al. 2010) and is also positively correlated with foliar nitrogen content (D. Gruner, *unpublished data*). Fertilization of *M. polymorpha* trees in the matrix increases foliar biomass relative growth rate and arthropod density (Gruner 2004). Although tree height does not directly correlate with species richness, tree height may affect diversity by increasing arthropod abundance. By necessity, kīpuka with higher abundance of individuals have a higher likelihood of containing more species (Gotelli and Colwell 2001, Chase et al. 2018). If kīpuka size correlates with an increase in resource availability or quality, we would expect a higher species richness purely on the basis of number of individuals. Kīpuka species density significantly increases with tree height across all spatial scales, further supporting that variation in resource availability or quality drives differences in arthropod abundance and consequently species richness. These results highlight that diversity patterns can be strongly affected by numbers of individuals (Gotelli and Colwell 2001).

Arthropod diversity at small scales was negatively correlated with kīpuka connectivity. Although we did not examine the cause for this negative relationship, metacommunity theory predicts a unimodal relationship between dispersal frequency and diversity (Mouquet and Loreau 2003, Leibold et al. 2004). When patches are isolated, increasing connectivity will promote local coexistence and allow for rescue effects, resulting in higher alpha diversity, as well as variation across patches in species composition and increased beta diversity. However, at higher dispersal levels or in well-connected landscapes, dispersal can increase metacommunity homogenization, reduce coexistence, and decrease local diversity. Furthermore, beta diversity would also decrease as a result of increased homogenization. Experimental work on zooplankton has found that dispersal can enhance or reduce species coexistence in metacommunities (Forbes and Chase 2002, Cottenie et al. 2003). Similarly, work on pitcher plants has shown a negative relationship between dispersal and local diversity in pitcher plant inquilines (Kneitel and Chase 2004). In line with the literature, we found small-scale variation in the effect size between diversity and connectivity measures, and low arthropod alpha diversity in highly connected kīpuka.

Our study exemplifies how the landscape structure, through patch configuration and nature of the matrix, interacts with focal organism characteristics to produce patterns in biodiversity. We do not find support for a species–area relationship in canopy arthropods, suggesting that *Metrosideros polymorpha* canopy arthropods are not dispersal-limited, in contrast to other taxa in this kīpuka landscape. Movement between kīpuka patches is likely not restricted enough to structure the makeup of these communities of organisms that disperse readily, can make use of sporadic low-quality resources in the matrix, and can use small kīpuka as stepping-stones. As such, our findings highlight the importance of considering the landscape perception of focal organisms. We suggest that providing connectivity through high numbers of smaller, proximate patches can be a promising management strategy to conserve biodiversity in patchy landscapes, but that within systems with a broad range of taxa, the ecological outcome may vary depending on scale of the organism. Our results show that the relationship between connectivity and diversity varies across relatively small spatial scales, and emphasize the utility of multiscale landscape analyses when dispersal information is unavailable or difficult to acquire. By shedding light on how habitat availability and connectivity vary across scales, multiscale approaches help us better understand the varied empirical results when studying biodiversity in patchy landscapes.

Acknowledgments

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