Effects of Natural Forest Fragmentation on a Hawaiian Spider Community

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ABSTRACT   The kipuka system, a network of forest fragments surrounded by lava flows on the island of Hawaii, offers an opportunity to study the natural, long-term fragmentation of a native ecosystem. We examined the impacts of habitat edges upon the community structure of nocturnally active native spiders, primarily in the genus *Tetragnatha*. We measured plant and spider species distributions across the edges of four small fragments and one large continuously forested area that were surrounded by a lava flow in 1855. Results indicated that an ≈20 m edge ecotone surrounds core forest habitat. Spider community structure changed across the edge, with a decrease in total species richness and diversity at the forest/lava boundary, and a change in the dominant taxon from native *Tetragnatha* (Tetragnathidae) to native *Cyclosa* (Araneidae). Severe habitat restrictions were found for some spider species. In addition, nearly all of the spiders captured were endemic species, and the few introduced species were limited to the younger and more open lava flows. Our results suggest that species responses to edges can vary, and that core habitat specialists may decline in fragmented conditions.

KEY WORDS   *Tetragnatha*, *Cyclosa*, edge effects, Hawaii, lava flows

THE FRAGMENTATION OF NATURAL landscapes is increasing worldwide as remaining natural areas are subdivided and converted for human uses. Therefore, understanding the ecological and evolutionary implications of fragmentation is of utmost importance. Fragmentation can disrupt an ecosystem in two major ways. First, decreases in the amount of natural area can elevate extinction rates and reduce overall levels of biodiversity (MacArthur and Wilson 1967, Trzcinski et al. 1999). Second, abiotic changes at the boundaries of remaining fragments, termed edge effects (Kapos 1989, Murcia 1995), can have complex population and community impacts. Edges can alter community structure by limiting the ranges of core habitat specialists and increasing the ranges and abundance of species distributed in the surrounding habitat and at fragment edges (Gascon et al. 1999). Edges can allow novel species interactions (Fagan et al. 1999, Laurance et al. 2001), as well as disrupt established ones (Estrada et al. 1998, Galetti et al. 2003). Over the long term, the isolation of populations of forest specialists may alter gene flow patterns and selection pressures, thus influencing the evolutionary trajectories of some organisms in fragmented landscapes (Lynam 1997, Bolger et al. 2000, Austen et al. 2001).

Numerous studies have examined edge effects of fragmentation in both tropical and temperate regions, particularly focusing on tropical forests (e.g., the Biological Dynamics of Forest Fragments project; see Lovejoy 1980). In many of the forest fragments under study, fragmentation has taken place relatively recently (within the past 20–50 yr) and has been of anthropogenic origin. Accordingly, much of the research presented in the literature has focused on documenting extinctions and defining structural changes that occur shortly after fragmentation events (Kapos 1989, Klein 1989, Bierregaard et al. 1992, Laurance et al. 2001, Bruna and Kress 2002). Predictions of longer-term ecological and evolutionary impacts have relied most heavily on theory (Gilpin and Soulé 1986) rather than empirical observations (but see Watson 2003). In addition, because most of the fragmentation under study is human induced, it can be difficult to tease apart the relative importance of fragmentation per se from the impact of human intrusion. Activities associated with human-related habitat fragmentation can attract invasive plants and animals, which in turn can influence the changes in habitat structure and species interactions that take place at habitat edges (Suarez et al. 2000, Harrison et al. 2001). As a result, the long-term physical changes in habitat structure and the fate of organisms in naturally fragmented forests are still largely unknown.

On the Big Island of Hawaii, natural fragmentation caused by volcanic activity has occurred repeatedly and can be accurately dated through geological methods. On Mauna Loa Volcano, lava flows dating back 400,000 yr have been a constant natural force of fragmentation, generating a mosaic of successional habitats (Carson and Clague 1995). Over 600 Mauna Loa

lava flows have been mapped in detail and dated using historical records and radiocarbon dating (Lockwood et al. 1988). A wealth of studies have taken advantage of this "chronosequence" of lava flows on Mauna Loa to investigate the state factors regulating primary succession, ecosystem development, and the spread of invasive species over time (Aplet and Vitousek 1994, Kitayama et al. 1995, Aplet et al. 1998, Clarkson 1998, Baruch and Goldstein 1999). We suggest that this lava flow chronosequence may also be useful in understanding the effects of habitat fragmentation over time.

Mature forests on Mauna Loa exist on older flows surrounded by younger barren flows, essentially creating a patchwork of forested islands (termed kipuka) of various sizes, shapes, and distances from each other. In this system of forest fragments, the long-term effects of edge formation and isolation can be examined in the absence of major human impacts. Forest regrowth on lava substrate can take considerably longer than in tropical soils deforested for agricultural uses (Kapos et al. 1997, Laurance et al. 2002). On newly formed flows, a mature closed canopy forest has been estimated to develop in 300–3,000 yr, with temporal differences depending on abiotic conditions (e.g., slope, aspect, altitude, and lava type) and biotic factors (e.g., presence of invasive species; Drake and Mueller-Dombois 1993, Clarkson 1998). In the kipuka system used in this study, fragments separated by lava over 100 yr ago remain easily distinguishable from the xeric plant communities present on the surrounding lava flows. In addition, the force responsible for fragmentation (molten lava) is abiotic, and the resulting fragments are in no way linked to human activities. The chosen study site is a mid-elevation site in a relatively remote area of the island, in which the forest is almost entirely native (Wagner et al. 1990). These characteristics, combined with the well-documented ages of the flows, make it possible to study the ecological effects and possible evolutionary consequences associated with fragmentation, with minimal human intervention, and over relatively long periods of time.

We investigated the long-term ecological effects of habitat edges on an important predatory component of Hawaiian forests: native, nocturnally active spiders chiefly in the genus *Tetragnatha* (Araneae: Tetragnathidae). Of the relatively few spider groups represented in Hawaii's native biota, the genus *Tetragnatha* has undergone the most impressive adaptive radiation, with several species often co-occurring in any one area, each with different microhabitat association (Gillespie 1991, 1992, 1994, 2002, 2004, Gillespie et al. 1997). Here, we characterize habitat edges independent of the spider community by documenting changes in plant species distributions and environmental conditions across a gradient from the interiors of fragments to the lava outside. We also measured spider abundance across these habitat edges to determine whether edges may limit species ranges and affect species interactions in the kipuka system.

Methods

Collections. We investigated a kipuka system that consists of mesic forest fragments surrounded by an 1855 lava flow originating from Mauna Loa Volcano (Fig. 1; general map coordinates: 19°37′40″ N and 155°21′15″ W). In April and May of 1998, we estimated plant and spider species abundance across the forest edge in four small forest patches (ranging in area from ≈1 to 2.6 ha) and in a large forest patch (area > 1,400 ha). These particular fragments were chosen because they are similar in age (ranging from ≈750–1,500 yr bp based on radiocarbon dating of lava substrates) and were most likely connected before the 1855 flow that currently surrounds them (Lockwood et al. 1988). Elevation ranges from 1,524 to 1,646 m, and all kipuka are of similar forest type, broadly categorized as mesic to wet *ohia* (*Metrosideros polymorpha*, Myrtaceae) forest with other native trees and a tree fern and native shrub understory (Jacobi 1990).

Within each small fragment, we sampled four transects spanning 30 m from the discernable tree boundary onto the lava flow and 30 m into the forest interior on the north, south, east, and west edges. In the large forest site, all four transects were placed along the north edge (which borders the 1855 flow), ≈20 m apart from one another. This distance between transects was chosen because it is comparable to the distances among transects in the interiors of the smaller fragments studied. Transects were limited to 30 m into the interiors of forest fragments because preliminary investigations of arthropod communities along transects of 100 m did not detect any changes beyond a 30-m distance (A.G.V., unpublished data). Each transect was divided into 12 equal sampling stations, 5 m in length by 2 m in width. All plants were identified and counted in each station. Spiders were collected along transects at each site between dusk and 2300 hours, the hours of peak activity for Hawaiian tetragnathids (Gillespie 1991, 1992, 1994, 2002, Gillespie et al. 1997). Spiders were located by visually searching all vegetation, rocks, and debris within each station. Based on initial timed trials of spider collecting at locations within kipuka interiors, search time was set at 5 min per station to standardize collecting efforts. Collected spiders were transported to the laboratory for identification based on morphological characteristics. Voucher specimens have been deposited in the Essig Museum of Entomology, University of California at Berkeley.

Abiotic conditions along transects were measured as follows. We estimated maximum and minimum temperature and humidity with digital gauges in the smallest patch and the nonfragmented forest (sites 4 and 5, respectively; Fig. 1). These two locations were chosen to maximize our ability to detect any changes in the environment associated with area effects as well as edge effects. Gauges were positioned at three shaded locations along two transects at each kipuka: 30 m inside of the forest at the forest edge and 30 m outside of the forest. Our goal was to measure the short-term microclimatic differences that spiders might respond
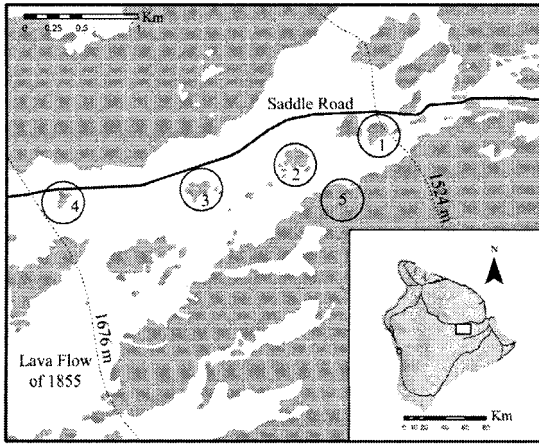
Fig. 1. Map of the study site, located on the Saddle Road, island of Hawaii. Forested areas are in gray; lava flows are in white. Kipuka 1–4 are small forest patches ranging in diameter from ≈100–250 m. Kipuka 5 is a large stretch of continuous forest. All kipuka are surrounded by an 1855 lava flow originating from Mauna Kea Volcano. Forests are classified as mesic to wet ohia forest with other native trees and a tree fern and native shrub understory (Jacobi 1990). Elevation ranges from 1,524 to 1,646 m. Map modified from USGS 7.5 min series (topographic), Upper Piihonua Quadrangle, Island of Hawaii, 1981.

to on a day-to-day basis, rather than determine long-term differences in temperature and humidity between the sites (see Vitousek et al., 1995 for long-term temperature and rainfall averages across Mauna Loa). Therefore, measurements were taken over a 24-h period during the time that spiders were collected.

Analyses. First, to explore patterns of covariance in our data and to determine the dominant axes describing plant and spider species distributions, we performed separate principal components analyses on plant and spider species abundance measured at each transect station. Spider data were log-transformed to meet normality assumptions. Loadings on the dominant axes were examined for biological meaning and possible correlations with transect and site characteristics. To estimate the vegetative edge size, plant species abundances were plotted versus location along transects. LOWESS smoothers, which combine weighted regression with robust measures of location for scatterplot points (Cleveland 1979), were used to visually assess habitat boundaries.

To determine abiotic changes across habitat (forest, edge, lava) and kipuka, ranges in temperature and humidity (the differences between maximum and minimum measurements) were compared by analysis of variance (ANOVA), using habitat, kipuka, and transect (nested within kipuka) as factors in each model. Ranges are presented instead of average temperature and humidity because they better represent the abiotic extremes that spiders inhabiting each habitat experienced. Statistical analyses were performed using the program Data Desk, Version 6.1 (Vellman 1997).

Habitat associations for spiders were explored in several ways. First, spider species richness and the Shannon diversity index (Magurran 1988) were calculated for each habitat type on each of the transects.
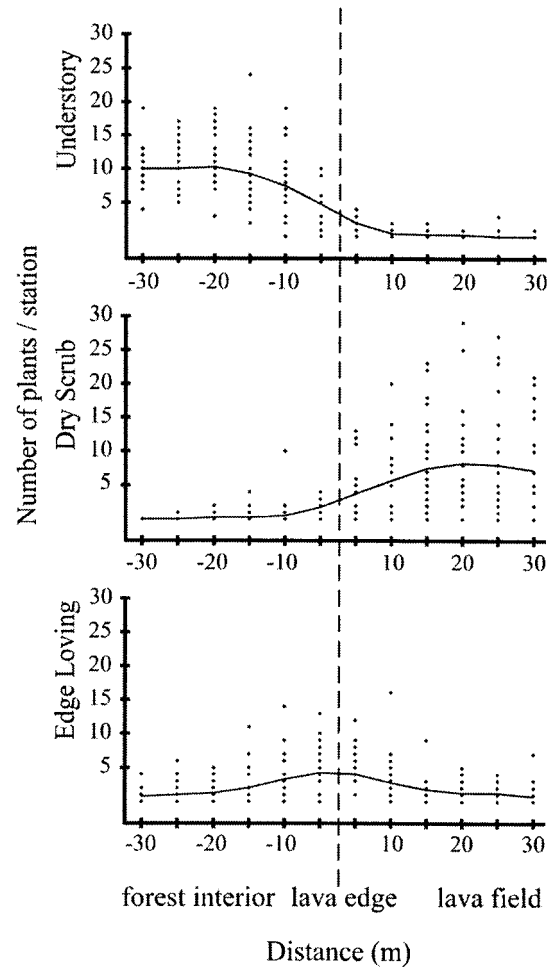

Fig. 2. Plots of plant species abundance versus transect station with lowess smoothing. Plant distributions were combined into three categories (Understory, Lava Colonizers, and Edge). "Understory" includes *Astelia menziesiana, Broussaisia arguta, Cheirodendron trigynum, Cibotium* sp., *Clermontia* sp., *Hedyotus* sp., *Ilex anomala, Labordia* sp., Lamiaceae sbfam. Prasioideae, *Myrsine lessertiana, Pelea clusiifolia, Peperomia* sp., *Psychotria hawaiensis, Rubus hawaiensis, Sadleria cyatheoides,* and *Smilax melastomifolia.* These species occur primarily under the main forest canopy. "Lava Colonizers" includes *Vaccinium reticulatum, Machaerina angustifolia, Lycopodium cernuum, Dubautia* sp., *Dicranopteris emarginata,* and *Coprosma ernodeoides.* These shrubs, sedges, club mosses, and ferns are found primarily outside of the forests. "Edge" includes *Styphelia tameiameiae, Vaccinium calycinum, Elaphoglossum crassifolium,* and *Coprosma* sp.. These are trees, shrubs, and ferns found primarily at the edges of forest patches. Overall, species abundances seem to change most dramatically between distances—10 and 10 m, suggesting that core forest and lava habitat types are separated by an edge of ≈20 m.

Table 1.   Results of ANOVA for ranges in temperature and humidity

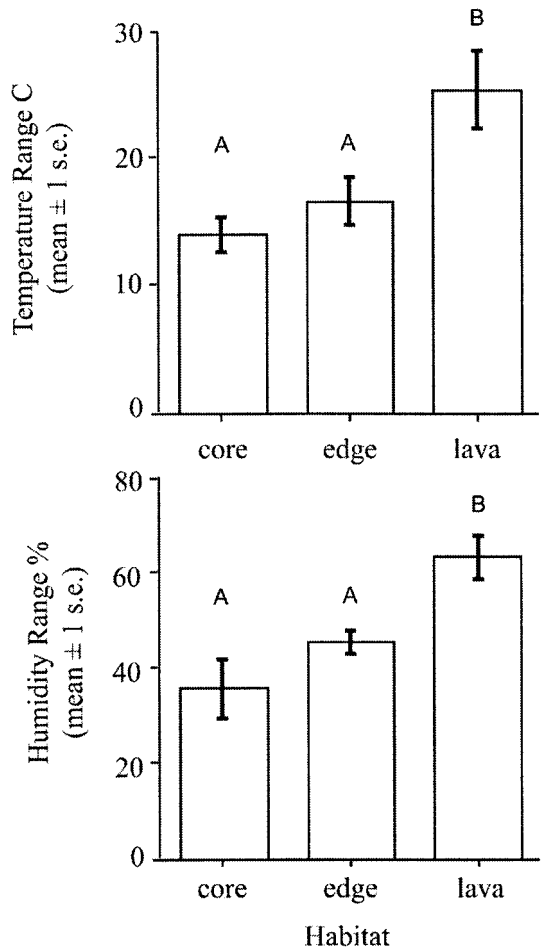| Factors	Temperature range				Humidity range		
	df	MS	F ratio	P	MS	F ratio	P
Kipuka	1	33.33	0.3774	0.6016	16.33	0.1059	0.7757
Transect (nested in kipuka)	2	88.33	3.7456	0.0880	154.17	2.3135	0.1800
Habitat	2	153.58	6.5124	0.0314	502.08	7.5344	0.0231
Error	6	23.58			66.64		

Diversity calculations were performed in the program EstimateS 5 (Colwell 1994). Differences between habitat types and among kipuka were tested using nested ANOVA with habitat type, kipuka, and transect (nested within kipuka) as factors. Spiders were also grouped by feeding ecology (which also corresponds to different genera and families). For each group, average abundance (averaged over kipuka) and 95% confidence intervals were plotted by transect collection station and examined to reveal any major shifts in habitat dominance along transects. Finally, a nested ANOVA was used to test for abundance differences among kipuka, transect stations (nested within kipuka), and transect direction (north, south, east, west) for each *Tetragnatha* species. Pairwise comparisons of spider species distributions were made using Tukey's least significant difference (LSD) posthoc tests.

Results

Changes in Plant Species Distributions and Determination of Edges. Demarcations between core forest, edge, and lava habitats were based on the dramatic changes in plant species distributions along transects. The primary axis from the principle components analysis of plant species, (comprising 11.1% of the variation in plant distributions) was highly correlated with the position of stations along a transect (Spearman rank correlation, $R = 0.796$, 238 df, $P \leq 0.0001$). Although this represented a small percentage of the total variation present in the dataset, the high correlation with station position suggested that the distance from the edge was an important factor describing covariation in plant species distributions. Outside of each forest patch, the vegetation was considerably sparse and contained relatively few species, including scattered dwarf *M. polymorpha* trees, native shrubs, and sedges. Inside the forest patches, vegetation was dense and composed of an upper canopy of *M. polymorpha,* other native trees and tree ferns, and a native understory. Using published habitat designations (Wagner et al. 1990), plant species were grouped into two main vegetative communities: lava colonizers and forest understory. On further examination of forest understory species, it was determined that some reached their highest abundances at the strict lava/forest edge (literally where the new lava flow stops), and these were categorized separately as edge plants. Scatterplots with lowess smoothers clearly showed a transitional zone between the two main vegetative communities that extended ≈10 m on each side of the

strict lava edge (Fig. 2). This area was also where the highest abundance of edge plants occurred. As a result, transects were divided into three habitat types for further analyses of spider distributions: the core forest, the lava habitat, and a 20-m span of edge habitat.

Changes in Microclimate. During the study, temperature and humidity ranges on the lava habitat were significantly greater than in the edge and core habitats

Fig. 3. Maximum and minimum temperature and humidity ranges for core, edge, and lava habitats. Graphs show mean values with SE. Lava habitats showed a significantly greater range in temperature and humidity than core and edge (temperature LSD posthoc tests: lava-core $P \leq 0.0154$, lava-edge $P \leq 0.0296$; humidity LSD posthoc tests: lava-core $P \leq 0.0134$, lava-edge $P \leq 0.0175$).

Table 2. Spider taxa found in all sites

Species	Web/feeding ecology[a]	Island[a]	Number collected[b]	Kipuka distribution[b]	Habitat distribution[b]		
					Core	Edge	Lava
Tetragnathidae							
Tetragnatha acuta	Nocturnal orb web	H,M	5	3,4,5	0	3	2
Tetragnatha n.sp. "golden dome"	Nocturnal orb web	H	63	All	28	30	5
Tetragnatha n.sp. "long clawed"	Nocturnal orb web	H	11	2,3,4,5	8	2	1
Tetragnatha hawaiensis	Nocturnal orb web	H	10	1,2,3,5	5	5	0
Tetragnatha brevignatha	Nocturnal cursorial	H,M	21	1,2,3,5	15	6	0
Tetragnatha quasimodo	Nocturnal cursorial	H,M,O	128	All	40	68	20
Tetragnatha anuenue	Nocturnal cursorial	H	76	All	57	17	2
Theridiidae							
Argyrodes n.sp.	Nocturnal cursorial	H,M	7	1,3,4	6	1	0
Theridion grallator	Mesh web	H,M,O	11	1,2,3,5	8	3	0
Theridion melinum	Mesh web	H,M,O	14	All	7	6	1
Araneidae[c]							
Cyclosa olorina/simplicicada	Persistant orb web	End H,M,O	78	All	0	19	58
Neoscona morpho-species 1	Persistant orb web	Adv-All?	6	2,3,4,5	0	1	5
Argiope morpho-species 1	Orb web	Adv-All?	1	3	0	0	1

R. Gillespie is currently describing new *Tetragnatha* species. *Argyrodes* n. sp. is currently being described by M. Rivera and R. Gillespie. Feeding Ecology: web-building spiders catch prey in webs while cursorial spiders run along or hang from vegetation, feeding on insects and other arthropods. *Argyrodes* prey exclusively on other spiders. For island distributions: H, Hawaii; M, Maui-Nui (Maui, Lanai, and Molokai); O, Oahu; All, Kauai, Oahu, Maui-Nui, and Hawaii.

[a] Based on previous studies (Simon 1900, Gillespie 1991, Gillespie et al. 1997).
[b] This study.
[c] All araneid spiders are identified to likely species or morphospecies based on morphology and historical records of species distributions in the Hawaiian Islands.

(Table 1; Fig. 3). Temperature and humidity fluctuated greatly on lava habitat, but were relatively stable at the edge and core of the forest kipuka. The range difference in temperature reflected warmer daytime and colder night temperatures on lava. Differences in humidity ranges were caused by large humidity fluctuations with prevailing precipitation and temperature on lava compared with consistently high humidity within the forest. There were no significant differences between kipuka for either temperature or humidity and no higher-level interactions (Table 1).

Changes in Spider Distributions. Thirteen spider species were collected, including seven endemic Hawaiian species in the genus *Tetragnatha* (Tetragnathidae), one endemic *Argyrodes* (Theridiidae), two endemic *Theridion* (Theridiidae), one endemic *Cyclosa* (Araneidae), and two non-native araneids in the genera *Neoscona* and *Argiope* (Table 2). Approximately 97% of all individuals belonged to endemic Hawaiian taxa, with the remaining 3% adventive to the islands (Nishida 1997). Spider species distributions varied with distance from the edge. As found with plants, in

the principle components analysis of species abundances, the principal axis (consisting of 10.7% of the variation in species distribution) was significantly correlated with station position along a transect (Spearman rank correlation, $R = -0.698$, 202 df, $P \leq 0.0001$). Although the primary axis describes only a small percentage of the total variation, the strong correlation with transect position established that distance from the fragment edge was an important variable explaining variation in spider species distributions. In addition, the ANOVA revealed significant effects of transect station and species on the number of spiders collected, but no effect of transect direction (Table 3). Higher-level interactions between kipuka, species, and transect station were also significant. From this test, we concluded that spider species abundance varied significantly across the habitat edge, but not with edge aspect, and that some species were patchily distributed among remnant forest fragments.

Changes in spider species composition were summarized in terms of species richness and diversity. Both richness and diversity were significantly lower in the lava

Table 3. Results of ANOVA for spider abundance

Factors	Spider abundance			
	df	MS	F ratio	P
Kipuka	4	0.238063	0.6394	0.6366
Station (nested in kipuka)	55	0.372308	1.8825	0.0001
Transect direction	3	0.297659	1.8825	0.2442
Species	12	8.12033	21.865	0.0001
Kipuka × transect direction	6	0.272466	1.2914	0.2683
Station × transect direction	98	0.210983	1.0668	0.3128
Kipuka × species	48	0.820924	2.2105	0.0001
Station × species	660	0.371381	1.8779	0.0001
Transect direction × species	36	0.154367	0.78054	0.8219
Error	1,705	0.197769		

Table 4. Results of ANOVA for spider diversity and richness

Source	df	Shannon Diversity index			Species richness		
		MS	F ratio	P	MS	F ratio	P
Kipuka	4	0.2053	1.135	0.3860	1.9489	1.999	0.1587
Transect (kipuka)	12	0.1809	1.619	0.1358	0.9745	0.684	0.7536
Habitat	2	2.2085	19.762	≤0.0001	26.8824	18.878	0.0001
Error	32	0.1118			1.4240		

habitat than in the edge and core habitats. Edge and core habitats did not differ significantly from one another. There were no significant differences in spider diversity and richness among kipuka, and no higher-level interactions were apparent (Table 4; Fig. 4).
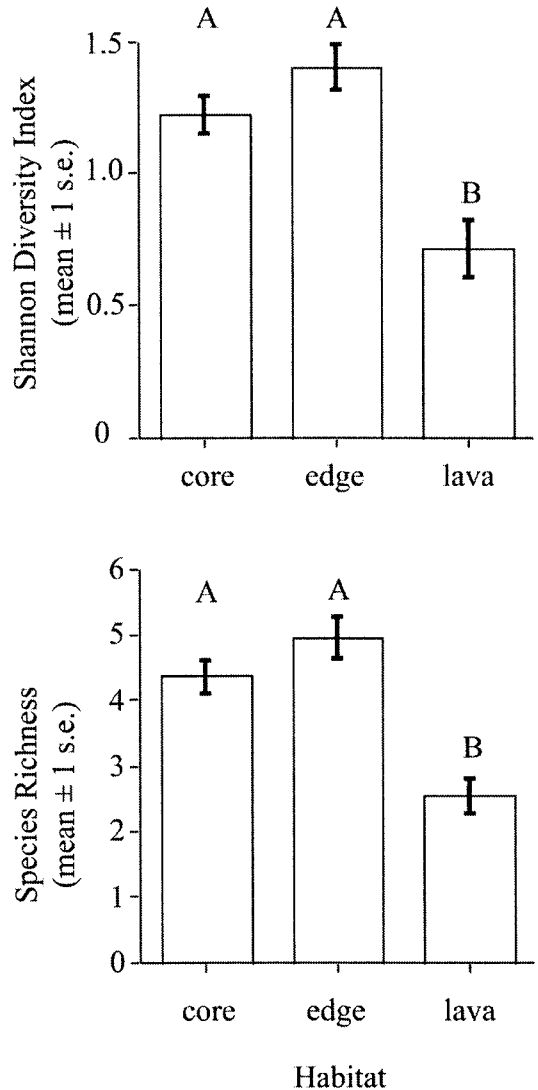
The drop in species richness and diversity in lava habitat reflects changes in foraging strategy and transitions between higher taxonomic groups that also occurred across this boundary. Within the forest core and edge habitats, endemic *Tetragnatha* spiders were the most abundant, with some endemic *Theridion* and *Argyrodes* species present in lower densities. The endemic *Cyclosa* dominated the lava habitat; in addition, there were a small number of individuals in the nonnative genera *Neoscona* and *Argiope.* When spiders were grouped by foraging behavior, cursorial species (*Tetragnatha* and *Argyrodes*) were mostly found within the core forest and edge habitat and decreased in abundance in the lava habitat (Fig. 5A). Similarly, nocturnal web-building spiders (*Tetragnatha*) occurred in somewhat similar abundance throughout the core forest and edge, but decreased in the lava habitat (Fig. 5C). In contrast, persistent web builders (*Cyclosa, Argiope,* and *Neoscona*) were almost completely absent from core forest habitat, increased in abundance through the vegetative edge, and reached their highest abundance on the more recent lava flows (Fig. 5B).

Fine scale differences among *Tetragnatha* species were also noted. Within *Tetragnatha,* we grouped species that showed similar patterns of abundance and distribution among transect stations and kipuka based on LSD posthoc comparisons of species from the ANOVA of spider abundance. *Tetragnatha* species fall into three distinct categories (Table 5): (1) those that were rare, found in a limited habitat range (either core and edge habitats, or for *Tetragnatha acuta,* lava and edge habitats) and absent from one or more kipuka; (2) those that were abundant, found mainly in core and edge habitats and found in all kipuka; and (3) one species (*Tetragnatha quasimodo*) that was abundant, distributed across forest, edge and lava habitats, and found in all kipuka.

Discussion

Our results corroborate some findings in other fragmentation studies that have examined the biological impacts of edges in tropical and temperate ecosystems (reviewed in Harrison and Bruna 1999, Laurance et al. 2002). In the context of other studies, our work may suggest that edge size decreases over time, or alternatively, that edges are narrower in cases where spe-

cies are well adapted to disturbance by fragmentation. Our study strongly indicates that species with different habitat preferences will respond differently to

Fig. 4. Spider species richness and diversity for core, edge, and lava habitats. Graphs show mean values with SE. Lava habitat had significantly lower species diversity and species richness than core and edge habitats (Shannon index LSD posthoc tests: lava-edge $P \le 0.0000$, lava-core $P \le 0.0001$; species richness LSD posthoc tests: lava-edge $P \le 0.0000$, lava-edge $P \le 0.0000$).
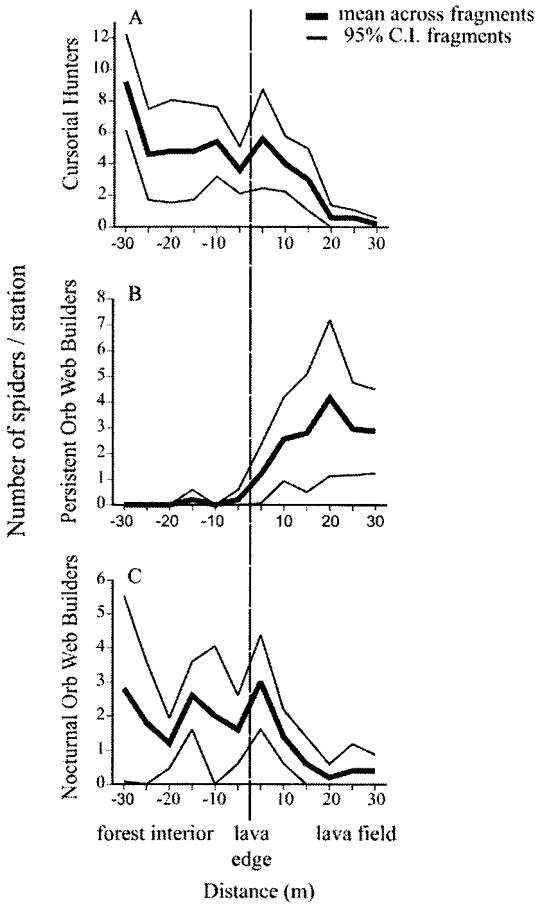
Fig. 5. Changes in spider abundance with distance averaged over fragments. Spiders groups are as follows. (A) Cursorial hunters: *Tetragnatha quasimodo*, *T. brevignatha*, *T. anuenue*, and *Argyrodes*. (B) Nocturnal web-builders: *Tetragnatha* n. sp. "golden dome," *T.* n. sp. "long-clawed," *T. hawaiiensis*, *T. acuta*. (C) Persistent orb web builders: *Cyclosa olorina/simplicicada*, *Neoscona*, and *Argiope*.

Edge Size. Plant communities changed across an edge boundary of ≈20 m surrounding forest patches. This edge extent is smaller than those of most other published studies conducted in tropical and temperate forests that have estimated edges of 40–100 m surrounding forest fragments (Lovejoy 1986, Murcia 1995). One possible reason for the difference is that wider edges are associated with newly formed fragments. In the Biological Dynamics of Forest Fragments Project, 6 mo after a fragmentation event, forest edges were sharply defined with measurable changes in temperature and humidity reaching at least 40 m in to the remaining forest (Kapos 1989). At 5 yr after isolation, reserve interiors were noticeably darker and more humid than in the first year, and it was predicted that over time, edge effects would stabilize, producing a band of modified vegetation or ecotone (Lovejoy 1986, Kapos et al. 1997). In their work on tropical gallery forests (naturally occurring forest fragments formed during the Pleistocene), Kellman et al. (1996, 1998) determined that edge effects caused by changes in light levels at the natural borders of these forests penetrated only the first 10–15 m. Our estimate of edge size in Hawaiian kipuka seems to fit somewhere in between the extremes of newly formed and extremely old fragments. Alternatively, the relatively narrow edges measured may be a characteristic of lava flows regardless of edge age, reflecting the fact that these communities are adapted to frequent lava disturbance. Consequently, we feel that changes in edge size over time merit further investigation. Given that lava flows of various ages exist across the island of Hawaii, this could be accomplished in future studies.

Spider Responses to Edges. Spider responses to the vegetative edge surrounding fragments varied with foraging behavior and species. Persistent web-building spiders (consisting mainly of endemic *Cyclosa*) increased in abundance in edges and reached their greatest numbers in lava habitat. Nocturnal web builders and cursorial species (mainly *Tetragnatha*) maintained high abundances throughout the core forest and edge habitat, decreasing only on lava flows. This pattern was broadly reflected in overall species richness and diversity. Both were slightly (although not significantly) higher in edge habitats and dropped dramatically on surrounding lava flows because of the addition of *Cyclosa* in edge habitat and the loss of most

edges. Additionally, the age and natural form of fragmentation allow us to further expand our discussion to address the evolutionary impacts of long-term fragmentation and the temporal component of invasions in Hawaii.

Table 5. *Tetragnatha* species grouped by abundance and distribution

	A	B	C
Species	*T. acuta* *T. brevignatha* *T.* "long-clawed" *T. hawaiensis*	*T.* "golden dome" *T. anuenue*	*T. quasimodo*
Kipuka distribution	Absent from one or more kipuka	All kipuka	All kipuka
Habitat Distribution	Mainly core and edge (*T. acuta* edge and lava)	Mainly core and edge	Core, edge, lava
Abundance	Low	High	High

Based on LSD posthoc tests, species in different groups (A–C) are significantly different from one another ($P \leq 0.05$; adjusted for multiple comparisons).

other species in lava habitat. Investigations of spider fragmentation responses have often found an increase in species numbers across edges as contrasting habitats intergrade and species mix (Bedford and Usher 1994, Luczak 1996).

The shift in dominance from *Tetragnatha* to *Cyclosa* in lava habitats is most likely caused by the drastic difference in habitat structure and changes in the abiotic conditions across this boundary. Hawaiian *Cyclosa* build webs that are markedly different from those of web-building *Tetragnatha*, with higher tension, a larger number of radii, long sticky spirals, and a high degree of asymmetry (Blackledge and Gillespie 2002). Because web architecture is directly related to how spiders use habitat and prey resources (Shear 1986, Blackledge and Wenzel 1999, Blackledge et al. 2003), this difference strongly suggests that *Cyclosa* and *Tetragnatha* target different prey and microhabitats. Within *Tetragnatha*, only *T. acuta* seemed to be specialized on edge and lava habitats. Most others were limited primarily to core forest and edge habitats, and for a subset of these (*T. brevignatha*, *T. anuenue*, and *T.* n. sp. "long-clawed"), we found fewer specimens overall in edge habitat than in core habitat. In contrast, *T. quasimodo*, a habitat generalist, was found in all habitat types. Such marked differences in habitat specificity are not limited to Hawaiian *Tetragnatha.* A recent study of *Tetragnatha* spider distributions in the Great Smoky Mountains found similar patterns (Aiken and Coyle 2000). Of five *Tetragnatha* species studied, four were restricted to particular habitats (e.g., grassland, wetlands, forest), and one was common in all habitat types.

Habitat Restrictions and Genetic Isolation. Studies of older forest fragments, such as Hawaiian kipuka, can help to determine how fragmentation affects the long-term structure and dynamics of populations (Templeton et al. 1990). The first step in such a study is the documentation of habitat restrictions caused by fragmentation. We found that many *Tetragnatha* species are limited to the core and edge habitats that contain native understory plants and tree ferns and that are more stable in temperature and humidity than open lava (Table 5, groups A, except *T. acuta*, and B). Because these species cannot persist on the open lava, different kipuka may be biologically isolated from one another despite the relatively short distances between them. Studies of genetic population structure in *T. brevignatha* (Table 5, group A) and *T. anuenue* (Table 5, group B) revealed that populations in kipuka were genetically more differentiated than populations in continuous forest (Vandergast 2002, Vandergast et al. 2004). This suggests that gene flow among isolated kipuka is limited for these species. Isolation of populations may ultimately lead to their local extinction. Theory predicts that small, isolated populations of organisms may be more prone to extinction in individual fragments because of demographic and environmental stochasticity (Gilpin and Soulé 1986). Three of the seven *Tetragnatha* species captured (Table 5, group A) fit this rare species profile. They were

limited to forested areas, occurred in very low numbers, and were missing from some sites.

Invasive Species. A common generalization of habitat fragmentation is that it facilitates invasions of exotics by disrupting strong species interactions and creating empty niches for opportunistic invaders (Hobbs and Huenneke 1992). In Hawaii, invasions of exotic invertebrates are associated with fragmentation in areas converted for agricultural, industrial, and residential uses (Howarth 1991). However, in the kipuka system that we investigated, plant and spider communities seemed to be virtually free from the influences of invasive species. There were no known invasive plant species encountered along transects, and <3% of the spiders collected belong to non-native taxa. Furthermore, non-native spiders were found only on open lava habitat. The absence of non-native species may not be surprising, because fragmentation by lava flows can be viewed as a natural part of the disturbance regime on shield volcanoes (Carson and Clague 1995). In a recent examination of habitat disturbance and invasions, Sher and Hyatt (1999) suggested that historically consistent natural disturbances (e.g., floods, tree-falls, fire) are generally not associated with invasive species. However, not all lava flows on the island of Hawaii are free of invasions. For example, *younger* lava flows in Hawaii Volcanoes National Park are heavily invaded by a non-native nitrogen fixing tree, *Myrica faya* (Vitousek et al. 1987, Walker and Vitousek 1991), and the introduced fountain grass, *Pennisetum setaceum* (Loope et al. 1992). Other investigations of forests on Mauna Loa have concluded that alien plant species are more likely to appear in native habitats where additional disturbances occur (Aplet et al. 1998). These examples underscore that biological invasions are complex processes dependent on the temporal and spatial distributions of potential invaders as well as the environmental conditions of the habitat itself. The fact that the kipuka study site has remained relatively free of non-native plant and spider species is most likely because of its remote location and the timing of the lava flow "disturbance" relative to the timing of major human impacts on that part of the island. However, ongoing improvements to the Saddle Road bordering the site and increased ecotourism may lead to increased human impacts and an increase in non-native species.

Conclusions

The Hawaiian kipuka system provides an ideal model for investigating the long-term effects of fragmentation. It is clear that lava flows have shaped the structure of native plant and spider communities on the island of Hawaii. Our results support the following generalizations: (1) species are affected differently by fragmentation and (2) core habitat specialists tend to decline in fragmented conditions. The vast majority of fragmentation studies to date have focused on anthropogenic fragmentation that has occurred relatively recently. Studies of older, naturally fragmented sys-

tems provide important null models for interpreting anthropogenic effects and can provide insight into the long-term ecological processes that they disrupt.

References Cited

Aiken, M., and F. A. Coyle. 2000. Habitat distribution, life history and behavior of *Tetragnatha* spider species in the Great Smoky Mountains National Park. J. Arachnol. 28: 97–106.

Aplet, G. H., and P. M. Vitousek. 1994. An age altitude matrix analysis of Hawaiian rain-forest succession. J. Ecol. 82: 137–147.

Aplet, G. H., R. F. Hughes, and P. M. Vitousek. 1998. Ecosystem development of Hawaiian lava flows: biomass and species composition. J. Vegetation Sci. 9: 17–26.

Austen, M.J.W., C. M. Francis, D. M. Burke, and M.S.W. Bradstreet. 2001. Landscape context and fragmentation effects on forest birds in southern Ontario. Condor. 103: 701–714.

Baruch, Z., and G. Goldstein. 1999. Leaf construction cost, nutrient concentration, and net CO_2 assimilation of native and invasive species in Hawaii. Oecologia (Berl.). 121: 183–192.

Bedford, S. E., and M. B. Usher. 1994. Distribution of arthropod species across the margins of farm woodlands. Agric Ecosystems Environ. 48: 295–305.

Bierregaard, R. O., Jr., T. E. Lovejoy, V. A. Kapos, A. D. Santos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments: a prospective comparison of fragments and continuous forest. Bioscience. 42: 859–866.

Blackledge, T. A., and J. W. Wenzel. 1999. Do stabilimenta in orb webs attract prey or defend spiders? Behav. Ecol. 10: 372–376.

Blackledge, T. A., and R. G. Gillespie. 2002. Estimation of capture areas of spider orb webs in relation to asymmetry. J. Arachnol. 30: 70–77.

Blackledge, T. A., G. J. Binford, and R. G. Gillespie. 2003. Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae). Ann. Zool. Fennici. 40: 293–303.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecol. Appl. 10: 1230–1248.

Bruna, E., M., and W. J. Kress. 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). Conservation Biol. 16: 1256–1266.

Carson, H. L., and D. A. Clague. 1995. Geology and biogeography of the Hawaiian Islands, pp. 14–29. *In* W. L. Wagner and V. A. Funk (eds.), Hawaiian biogeography:

evolution on a hot spot archipelago. Smithsonian Institution Press, Washington, DC.

Clarkson, B. D. 1998. Vegetation succession (1967–89) on five recent montane lava flows, Mauna Loa, Hawaii. NZ J. Ecol. 22: 1–9.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. 74: 829–836.

Colwell, R. K. 1994. EstimateS 5 computer program. University of Connecticut, Storrs, CT.

Drake, D. R., and D. Mueller-Dombois. 1993. Population development of rain forest trees on a chronosequence of Hawaiian lava flows. Ecology. 74: 1012–1019.

Estrada, A., R. Coates-Estrada, A. A. Dadda, and P. Cammarano. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. J. Trop. Ecol. 14: 577–593.

Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. Am. Naturalist. 153: 165–182.

Galetti, M., C. P. Alves-Costa, and E. Cazetta. 2003. Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. Biol. Conserv. 111: 269–273.

Gascon, C., E. T. Lovejoy, R. O. Bierregaard, Jr., R. J. Malcolm, C. Stouffer Phillip, L. Vasconcelos Heraldo, F. W. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biol. Conserv. 91: 223–229.

Gillespie, R. G. 1991. Hawaiian spiders of the genus *Tetragnatha:* I. Spiny leg clade. J. Arachnol. 19: 174–209.

Gillespie, R. G. 1992. Hawaiian spiders of the genus *Tetragnatha:* II. Species from natural areas of windward east Maui. J. Arachnol. 20: 1–17.

Gillespie, R. G. 1994. Hawaiian spiders of the genus *Tetragnatha:* III. Tetragnatha acuta Clade. J. Arachnol. 22: 161–168.

Gillespie, R. G. 2002. Hawaiian spiders of the genus *Tetragnatha:* IV new, small species in the spiny leg clade. J. Arachnol. 30: 159–172.

Gillespie, R. G. 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science. 303: 356–359.

Gillespie, R. G., H. B. Croom, and G. L. Hasty. 1997. Phylogenetic relationships and adaptive shifts among major clades of *Tetragnatha* spiders (Araneae: Tetragnathidae) in Hawai'i. Pacific Sci. 51: 380–394.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction, pp. 19–34. *In* M. E. Soulé (ed.), Conservation biology. Sinauer, Sunderland, MA.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography. 22: 225–232.

Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. Biol. Conserv. 100: 45–53.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Biol. Conserv. 6: 324–337.

Howarth, F. G. 1991. Impacts of alien land arthropods and molluscs on native plants and animals in Hawaii, pp. 149–179. *In* C. P. Stone and J. M. Scott (eds.), Hawaii's terrestrial ecosystems: preservation and management. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu, HI.

Jacobi, J. D. 1990. Distribution maps, ecological relationship, and status of native plant communities on the island

of Hawaii. U.S. Government Publications, Washington DC.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. J. Trop. Ecol. 5: 173–185.

Kapos, V., E. Wandelli, J. L. Camargo, and G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia, pp. 33–44. In W. F. Laurance and J.R.O. Bierregaard (eds.), Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL.

Kellman, M., R. Tackaberry, and J. Meave. 1996. The consequences of prolonged fragmentation: lessons from tropical gallery forests, pp. 37–58. In J. Shelhas and R. Greenberg (eds.), Forest patches in tropical landscapes. Sinauer, Sunderland, MA.

Kellman, M., R. Tackaberry, and L. Rigg. 1998. Structure and function in two tropical gallery forest communities: implications for forest conservation in fragmented systems. J. Appl. Ecol. 35: 195–206.

Kitayama, K., D. Mueller Dombois, and P. M. Vitousek. 1995. Primary succession of hawaiian montane rain forest on a chronosequence of eight lava flows. J. Vegetation Sci. 6: 211–222.

Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia [Brazil]. Ecology. 70: 1715–1725.

Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology. 82: 105–116.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16: 605–618.

Lockwood, J. P., P. W. Lipman, L. D. Petersen, and F. R. Warshauer. 1988. Generalized ages of surface lava flows of Mauna Loa Volcano, Hawaii. miscellaneous investigations. Series Map I-1908. U.S. Geological Survey, Reston, VA.

Loope, L. C., R. J. Nagata, and A. C. Medeiros. 1992. Alien plants in Haleakala national park, pp. 551–576. In C. P. Stone, C. W. Smith, and J. T. Tunison (eds.), Alien plant invasions in native ecosystems of Hawai'i: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, HI.

Lovejoy, T. E. 1980. Discontinuous wilderness: minimum areas for conservation. Parks. 5: 3–15.

Lovejoy, T. E. 1986. Edge and other effects of isolation on Amazon forest fragments, pp. 257–285. In M. E. Soulé (ed.), Conservation biology. Sinauer, Sunderland, MA.

Luczak, J. 1996. Plant-dwelling spiders of the ecotone between forest islands and surrounding crop fields in agricultural landscape of the Masurian Lakeland. Ekologia Polska. 43: 79–102.

Lynam, A. J. 1997. Rapid decline of small mammal diversity in monsoon evergreen forest fragments in Thailand, pp. 222–240. In F. W. Laurance and R. O. Bierregaard (eds.),

Tropical forest remnants: ecology, management and conservation of fragmented communities. University of Chicago Press, Chicago, IL.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10: 58–62.

Nishida, G. M. 1997. Hawaiian terrestrial arthropod checklist. Hawaii Biological Survey, Bishop Museum, Honolulu, HI.

Shear, W. A. 1986. Spiders, webs, behavior, and evolution. Standford University Press, Stanford, CA.

Sher, A. A., and L. A. Hyatt. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. Biol. Invasions. 1: 107–114.

Suarez, A. V., J. Q. Richmond, and T. J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. Ecol. Appl. 10: 711–725.

Templeton, A. R., K. Shaw, E. Routman, and S. K. Davis. 1990. The genetic consequences of habitat fragmentation. Ann. MO Botanical Garden. 77: 13–27.

Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecol. Appl. 9: 586–593.

Vandergast, A. G. 2002. Ecology and genetics of habitat fragmentation in spiders of Hawaiian kipukas. ESPM, Divison of Insect Biology. University of California, Berkeley, CA.

Vandergast, A. G., R. G. Gillespie, and G. K. Roderick. 2004. Influence of volcanic activity on the population genetic structure of Hawaiian Tetragnatha spiders: fragmentation, rapid population growth and the potential for accelerated evolution. Molec. Ecol. 13: 1729–1743.

Vellman, P. F. 1997. Data Desk computer program, version 6.1 for Macintosh. Data Description Inc., Ithaca, NY.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by Myrica faya alters ecosystem development in Hawaii USA. Science. 238: 802–804.

Vitousek, P. M., G. H. Aplet, J. W. Raich, and J. P. Lockwood. 1995. Biological perspectives on Mauna Loa Volcano: a model system for ecological research, pp. 117–125. In J. M. Rhodes and J. P. Lockwood (eds.), Mauna Loa revealed: structure, composition, history and hazards. American Geophysical Union, Washington, DC.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. Manual of the flowering plants of Hawaii. University of Hawaii Press, Bishop Museum Press, Honolulu, HI.

Walker, L. R., and P. M. Vitousek. 1991. An invader alters germination and growth of a native dominant tree in Hawaii. Ecology. 72: 1449–1455.

Watson, D. M. 2003. Long-term consequences of habitat fragmentation—highland birds in Oaxaca, Mexico. Biol. Conserv. 111: 283–303.