Plant Dispersal, Introduced Species, and Vegetation Change in the South Pacific Kingdom of Tonga[1]

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Abstract: Dispersal guilds hold key ecological implications for the vegetation history of islands. This study considers dispersal vectors in conjunction with species origin and growth form to characterize vegetation dynamics on the islands of Tonga in the South Pacific. Data for over 700 species compiled from published literature on the plants of Tonga support a comparative study of dispersal mechanisms and growth forms for native flora, species brought by Polynesian settlers, and taxa introduced since European contact. The indigenous flora, predominantly trees, is characterized primarily by endozoochorous (internal) dispersal through birds and bats. European introductions, primarily herbs, disperse commonly through epizoochorous (external) animal dispersal. Bat dispersal is most important for overstory indigenous and Polynesian trees and vines. In addition, rodents commonly eat seeds of native rain forest trees. The understory, which is overwhelmingly introduced, consists of wind-dispersed and externally animal-dispersed species, which are often early successional. Rain forest thinning encourages establishment of wind-dispersed species and nonnatives. Thus, the prospect of sustained native flora in Tonga would be enhanced by the preservation of bats, a particularly important dispersal vector for indigenous and endemic species, and by the eradication of introduced rats.

The arrival and dispersal of island plants characteristically features long-distance transport by wind, water, or avifauna (e.g., Carlquist 1974), followed by local dispersal within islands, primarily by animals. Birds and bats are centrally important biotic dispersal agents (Banack 1998, Corlett 1998, Muscarella and Fleming 2007), particularly in tropical island ecosystems (Whittaker and Jones 1994). Dispersal of seeds is crucial for plant reproduction and regeneration. A dispersal guild consists of a group of plant species that share common means of dispersing their seeds or fruits away from parent plants. Dispersal vectors include both abiotic (e.g., wind and water) and biotic (animal) distribution methods.

The indigenous and endemic flora of Tonga was altered by the arrival of Polynesian peoples approximately 3,000 yr ago, leading to a suite of ecological transitions (Fall 2005). These settlers transported pigs, herbaceous root crops, and trees for food and building material (Whistler 1991), while introducing, less intentionally perhaps, the Polynesian rat (*Rattus exulans* [Dye and Steadman 1990]). This transition led to the introduction of several bird species, as well as the extinction of numerous land birds (see Steadman 1995, 1998), including the two largest pigeons of Tonga, the Immense Pigeon (*Ducula*, undescribed species) and David's Pigeon (*Ducula* cf. *david*) (Steadman 2006), and the extirpation of one of two native species of fruit bats, the Samoan flying fox (*Pteropus samoensis*) (Koopman and Steadman 1995). Thus, the arrival of Polynesians may have triggered pervasive ecological alterations in Tonga through

the disruption of dispersal guilds, especially those involving birds and bats (Meehan et al. 2002).

A further array of plants and animals has been introduced to Tonga over the last three centuries since the first arrival of Europeans. New plants represent food sources (mostly trees and herbs), garden ornamentals, and weeds (Whistler 1991, 1995). Associated animal introductions include the domestic goat, the ship rat (*Rattus rattus*), the Norway rat (*Rattus norvegicus*), and several species of birds, leading to further ecological disruption. Seed predation in tropical forests, particularly by rats (as demonstrated on Polynesian islands [McConkey et al. 2003, Meyer and Butaud 2009, Prebble and Wilmshurst 2009]), has renewed the alteration of Tongan seed dispersal guilds. As one of many cases with ecological consequences, the Friendly Ground-Dove (*Gallicolumba stairi*) is restricted to some islands in Tonga that lack ship rats (Rinke 1991), although it does occur on the main island in Vava'u where ship rats have been observed (Twibell 1973, Steadman et al. 1999).

Dispersal adaptations provide basic reproductive and ecological information about plant species and ecosystems. Further, dispersal mechanisms also reflect life history characteristics of species. For example, early successional taxa often include wind-dispersed species, which establish themselves in disturbed sites (Brown 1992, Drezner et al. 2001), such as on Rakata Island in the Krakatau group, where wind-dispersed (anemochorous) species established before bird-dispersed (ornithochorous) species (Whittaker et al. 1989). A plant community's dispersal spectra also can reflect climatic conditions (e.g., Willson et al. 1990) as exemplified by the association of wetter environments with greater dispersal by birds than by wind (Armesto and Rozzi 1989). Thus, dispersal spectra provide critical insights into ecological relationships as they develop on an island. With Tonga's ecological legacy in mind, we consider plant dispersal in conjunction with species origin and growth form to portray the life history and shifting plant ecology that have shaped the modern flora of Tonga. Our study proposes that: (1) introduced plants will

have life history traits that differ from those of native taxa, thereby changing not only the composition of plant communities, but more importantly, the proportional representation of different dispersal guilds; and (2) dispersal guild distinctions (e.g., animal dispersal by epizoochory versus endozoochory) carry various ecological implications (e.g., niche, future establishment success), which will selectively favor the establishment not only of different plant species but of different growth forms and should be particularly apparent between overstory and understory species.

Study Area

The Kingdom of Tonga comprises a chain of over 170 islands in the South Pacific between about 23° and 15° S and between 173° and 177° W lying southwest of Samoa and east of Fiji (Figure 1). These islands lie at the eastern edge of the Austral-Indian Plate. Tonga consists of three main limestone island groups in a north-south alignment, which include Tongatapu, Ha'apai, and Vava'u, that formed as part of the forearc belt of the Tongan-Kermadec Trench system between <1 and 10 million yr ago (Dickinson 2001). Subduction of the Pacific Plate formed the younger (and still active) volcanic islands of Tonga that lie to the west of the uplift limestone platform in a second island chain from Niuafo'ou in the north to 'Ata in the south. The largest limestone islands are Tongatapu (261 km²; 80 m elev.) and 'Eua (81 km²; 312 m elev.) in the Tongatapu island group, and 'Uta Vava'u (ca. 96 km²; 200 m elev.) in the Vava'u island group. Tofua in the Ha'apai island group last erupted in 1959 and is the largest volcanic island (47 km²; 558 m elev.).

Tonga's position in the track of the southeastern trade winds affords a mild tropical climate with mean annual temperatures between 21°C and 23.5°C and yearly precipitation usually between about 1,780 and 2,340 mm (Thompson 1986). Mean monthly precipitation and temperature values are slightly higher in the austral summer and are higher in the northern part of Tonga than in the southern islands. Tropical cyclones occur in the late summer (Woodroffe 1983, Franklin
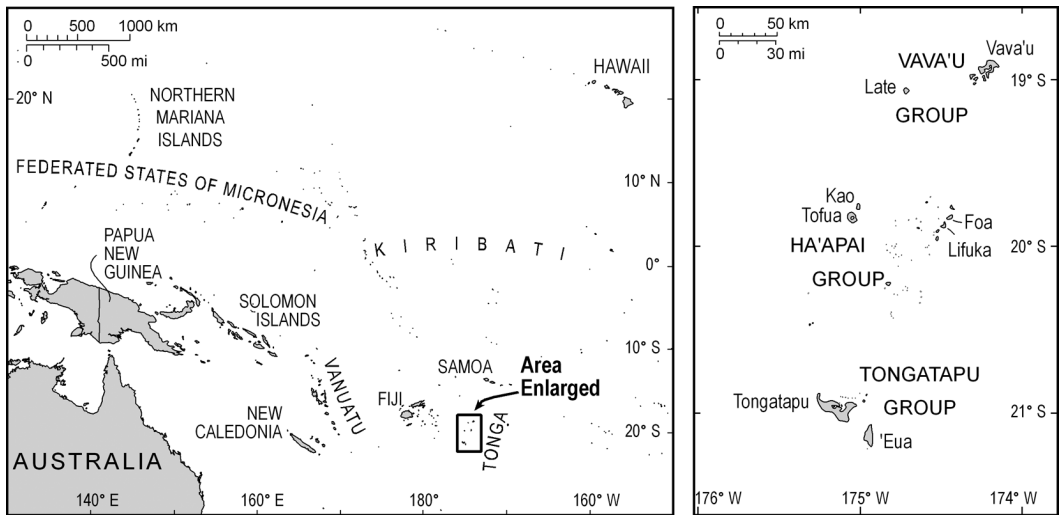
Figure 1. Location of the Kingdom of Tonga in the South Pacific Ocean; inset shows main islands in Tonga (map by Barbara Trapido-Lurie).

et al. 2004). The vegetation of Tonga has strong affinities to, and probably was dispersed from, the much larger and higher islands of Fiji, approximately 750 km west of Tonga, or from Samoa, about 900 km to the north. The larger size and elevation and greater age of Fiji's main islands, Viti Levu (over 10,000 km²; 1,394 m elev.) and Vanua Levu (over 5,000 km²; 1,111 m elev.), provide likely source areas for the Tongan flora (Smith 1979–1991). Additional floral source areas could be the relatively young islands of Samoa, including the largest islands of Savai'i (1,694 km²; 1,858 m elev.) and Upolu (1,125 km²; 1,100 m elev.), which provide greater size, elevation, and habitat and species diversity than found on Tonga (Whistler 1992*b*).

Several general discussions describe the vegetation and biogeography of the Tongan islands (Yuncker 1959, Sykes 1977, 1981, Stoddart 1992, Whistler 1992*a,b*, Mueller-Dombois and Fosberg 1998). Numerous botanical inventories document plant species for the island groups of Tongatapu (Palmer 1988, Wiser et al. 2002), 'Eua (Drake et al. 1996), Vava'u (Franklin et al. 1999, Steadman et al. 1999, Franklin 2003), Tofua, and Kao (Park and Whistler 2001), as well as for multiple is-

land groups (Franklin et al. 2006). Although there is no complete flora of Tonga, Park and Whistler (2001) estimated that about 450 of the plant species are indigenous or endemic and approximately 240 species represent introductions by Polynesians or later settlers following European contact. Polynesian populations reached Tonga by 2,850 yr B.P. (Burley 1998). Initial European contact involved Dutch sailors in the 1600s, followed by more substantial interactions with James Cook and his crews between 1773 and 1777, and missionary settlement beginning in the late 1700s (Whistler 1991). Thus, the vegetation of Tonga has been altered substantially by repeated human colonization (Fall 2005, 2010).

Inventories of extant and extinct birds and bats were made on 'Eua (Rinke 1987, Steadman 1993, Koopman and Steadman 1995), Ha'apai (Steadman 1998), Vava'u (Steadman and Freifeld 1999, Steadman et al. 1999, McConkey et al. 2004), Niuafo'ou (Rinke 1986, 1991), 'Ata and Late (Rinke 1991), and for multiple islands (Grant 1998, Steadman 2006). Several bird species were introduced by Polynesians, including the domestic chicken (*Gallus gallus*), the Pacific Pigeon (*Ducula pacifica*), a widely distributed and im-

portant frugivore, and the Red Shining Parrot (*Prosopeia tabuensis*). Other extant frugivorous birds common in Tonga include the Purple-Capped Fruit-Dove (*Ptilinopus porphyraceus*) and the Polynesian Starling (*Aplonis tabuensis*). Two frugivores have been extirpated from Vava'u in the past 150 yr: the Many-Colored Fruit-Dove (*Ptilinopus perousii*), and the Blue-Crowned Lorikeet (*Vini australis*) in the twentieth century (Steadman and Freifeld 1999). Further, a survey in 1995 showed that *Gallicolumba stairi* was extremely rare on the largest island in Vava'u (Steadman and Freifeld 1999). Omnivorous species in Tonga also capable of dispersing seeds include, or have included, the Polynesian Triller (*Lalage maculosa*), the Fiji Shrikebill (*Clytorhynchus vitiensis*) (now extirpated from Vava'u), and the endemic Tongan Whistler (*Pachycephala jacquinoti*). The nectar-sipping Wattled Honeyeater (*Foulehaio carunculata*) is an important pollinator of the indigenous flora. Based on paleontological data from 'Eua and Ha'apai, approximately 25–30 species of land birds lived in Tonga before human arrival (Steadman 1993, 1995, 1998). After European contact, historical introductions include the Red-Vented Bulbul (*Pycnonotus cafer*), the European Starling (*Sturnus vulgaris*), and the Rock Dove (*Columba livia*). In addition to the land birds, the Tongan fruit bat or flying fox (*Pteropus tonganus*) is capable of dispersing seeds and fruits of plants in Tonga; the Samoan fruit bat (*Pteropus samoensis*) has been extirpated from the islands (Koopman and Steadman 1995).

MATERIALS AND METHODS

This study utilizes data for 737 plant species, compiled by the authors from published studies of the vegetation of Tonga (Yuncker 1959, Sykes 1977, 1981, Palmer 1988, Whistler 1991, 1992*a,b*, 1995, Stoddart 1992, Drake et al. 1996, Mueller-Dombois and Fosberg 1998, Franklin et al. 1999, Steadman et al. 1999, Park and Whistler 2001, Wiser et al. 2002, Franklin 2003, Franklin et al. 2006). Based on this documentation, we determined growth form, origin, and dispersal mechanism for these species in Tonga. Species used in this study are mainly angiosperms but also incorporate a few gymnosperms (including the native tree *Podocarpus pallidus* and introduced *Pinus caribaea*) and pteridophytes. Species origins were identified and categorized as endemic, indigenous, Polynesian introductions, or European introductions, following Whistler (1991, 1992*a,b*, 1995). Although many introduced plants have come from Asia, Africa, or the Americas, nonnative introductions that arrived after European contact are referred to here as "European" in contrast to "Polynesian" plants that arrived with the earliest indigenous settlers.

Dispersal vectors for Tongan plants were derived first from the classic volumes by Ridley (1930) and van der Pijl (1982), followed by other sources, such as Guppy (1906) and Carlquist's studies (1967, 1974) of dispersal on Pacific islands. We identified dispersal mechanisms for these species based on more than 60 primary, peer-reviewed articles and books. Our methods are described, and many specific dispersal references are listed, in Fall et al. (2007). Dispersal mechanisms include water (hydrochory), wind (anemochory), internal animal dispersal (endozoochory), external animal dispersal through adhesion (epizoochory), bats (fruit bats or flying foxes) (chiropterochory), birds (ornithochory), rodents, which may practice seed predation rather than dispersal (Osunkoya 1994, Abe 2007, Meyer and Butaud 2009, Grant-Hoffman and Barboza 2010), and human cultivation (intentional dispersal). The term "rodent" here refers to rats, rather than the introduced mouse. Most plants in Tonga have multiple dispersal mechanisms (Fall et al. 2007), and all dispersal vectors for any given taxon are incorporated in this study. Thus, the frequencies for the dispersal mechanisms pertaining to origin or growth form may total more than 100%. Growth forms, also determined from published literature on the plant species of Tonga, are designated as graminoids (grasses, sedges, and rushes), herbs, shrubs, vines and lianas, and trees. Taxonomic nomenclature follows Smith (1979–1991) and Whistler (1991).

We are particularly interested in changes in the vegetation of Tonga that accompanied the arrival of Polynesian and, subsequently, European or later populations. Our data illus-

trate vegetation change effected by these colonists in a variety of ways, including two central hypotheses. We expected that the vegetation of Tonga shifted substantially according to dispersal syndromes and growth forms with these two waves of colonization. Thus, we used our data to test two central null hypotheses. The first null hypothesis maintains that the patterns of dispersal mechanisms for Polynesian plant introductions and for post-European arrivals did not differ significantly from those of endemic and indigenous (i.e., before human arrival) species. We tested this proposition by converting the species count for each dispersal mechanism among endemic and indigenous species to a proportion of the total endemic and indigenous species count. (For example, the proportion of wind dispersal among endemic and indigenous species is 14.6%.) Because the null hypothesis argues for no change in dispersal syndromes according to plant origin, we used the endemic and indigenous dispersal proportions to calculate expected counts for each dispersal mechanism among species introduced by Polynesians and after European contact. (For example, the dispersal count among Polynesian introductions totals 226. The observed Polynesian species count for wind dispersal is 14, but the null hypothesis leads to an expected count of 33, based on the proportion of wind-dispersed endemic and indigenous species $[226 \times 0.146 = 32.996]$). We assessed our first central null hypothesis with chi-square tests of the difference between observed and expected species counts according to dispersal mechanism for plant species introduced by Polynesians and for those brought after European contact. We employed chi-square analysis because our dataset is not normally distributed, making nonparametric tests such as chi-square preferable. Further, we included classified nominal data, as well as frequency data, both of which are ideally suited for chi-square analysis.

Similarly, our second central null hypothesis holds that the suite of plant growth forms found among Polynesian introductions and among European taxa did not differ significantly from those characteristic of endemic and indigenous species. To test this hypoth-

esis we converted the species count for each growth form among endemic and indigenous species to a proportion of the total endemic and indigenous species count. In this instance the null hypothesis argues for no change in the array of growth forms according to plant origin, so we used the endemic and indigenous growth form proportions to calculate expected counts for each growth form among species introduced by Polynesians and by Europeans. Accordingly, we assessed our second central null hypothesis with chi-square tests of the difference between observed and expected species counts according to growth form for plant species introduced by Polynesians and by Europeans.

<center>RESULTS</center>

Our study of dispersal mechanisms in Tonga revealed a variety of patterns related to plant origins (Tables 1 and 2). A chi-square goodness of fit test revealed a significant difference across eight dispersal mechanisms for endemic and indigenous versus Polynesian plant species ($\chi^2 = 43.2$, df = 7, $P < .0001$), refuting the null hypothesis that dispersal mechanisms do not differ between those origin types. Likewise, a chi-square test showed a significant difference in dispersal mechanisms for endemic and indigenous versus European introductions ($\chi^2 = 151$, df = 7, $P < .0001$), again refuting the null hypothesis. Indeed, our results reveal substantial shifts in dispersal mechanisms with the introduction of plants, first by Polynesian colonists, then in the wake of European contact.

Among abiotic dispersal mechanisms, more plant species are dispersed by water than by wind, regardless of origin. This tendency is slight among native species and most noticeable for Polynesian introductions. When considering species adapted for animal (nonhuman) dispersal, plants of all origins are dispersed most commonly by birds, followed by bats and rodents, and more often by internal animal dispersal than external animal dispersal. In particular, seeds of endemic species ($n = 13$ taxa, data not shown in Table 1) are disproportionately dispersed by animals (by endozoochory [12 taxa], birds [11], or bats

TABLE 1

Number of Tongan Plant Species Dispersed by Each Mechanism According to Origin Type

Origin		Dispersal Mechanism							
		Water	Wind	Internal	External	Bat	Bird	Rodent	Hum Cult
E&I	Observed	137	127	198	57	98	217	24	14
Poly[a]	Observed	35	14	44	12	20	49	8	44
	Expected	35	33	51	15	25	56	6	4
Euro[b]	Observed	137	96	170	89	44	173	19	148
	Expected	138	128	199	57	98	218	25	14

Note: Origin types include endemic and indigenous species (E&I, $n = 364$), and Polynesian introductions (Poly, $n = 64$) and species introduced after European (Euro, $n = 309$) contact. Dispersal mechanisms include water; wind; internal animal dispersal (Internal); external animal dispersal through adhesion (External); dispersal involving bats, birds, and rodents; and human cultivation (Hum Cult). Most species are dispersed by more than one mechanism.
  [a] Chi-square goodness of fit test for observed versus expected species counts by dispersal mechanism for Polynesian introductions: $\chi^2 = 43.2$, df = 7, $P < .0001$.
  [b] Chi-square goodness of fit test for observed versus expected species counts by dispersal mechanism for European introductions: $\chi^2 = 151$, df = 7, $P < .0001$.

TABLE 2

Number of Tongan Plant Species in Each Growth Form According to Origin Type

Origin		Growth Form				
		Tree	Vine	Shrub	Herb	Grass
E&I	Observed	128	45	30	41	16
Poly[a]	Observed	25	4	5	20	5
	Expected	29	10	7	9	4
Euro[b]	Observed	60	27	48	113	37
	Expected	140	49	33	45	18

Note: Origin types include endemic and indigenous (E&I) species and Polynesian (Poly) and European (Euro) introductions.
  [a] Chi-square goodness of fit test for observed versus expected species counts by growth form for Polynesian introductions: $\chi^2 = 7.48$, df = 4, $P = .112$.
  [b] Chi-square goodness of fit test for observed versus expected species counts by growth form for European introductions: $\chi^2 = 77.0$, df = 4, $P < .0001$.

[8]), rather than by wind (2) or water (1). Native species (including both endemic and indigenous taxa) and Polynesian introductions are characterized by bat dispersal, rather than external animal dispersal, which is more prevalent among plants introduced after European contact. Among introduced plants, the dispersal influences of rats (and assumed predation) are most pronounced among Polynesian rather than European species. Human-cultivated species tend to be Polynesian and European introductions, but only the native flora is dispersed more commonly by bats than through human cultivation.

The growth forms of Tongan species also vary systematically according to origin and dispersal mechanisms. A chi-square goodness of fit test shows a significant difference across five vegetation growth forms for endemic and indigenous versus European plant species ($\chi^2 = 77.0$, df = 4, $P < .0001$), refuting the null hypothesis that these origin types do not differ according to growth forms. However, a chi-square test of endemic and indigenous species versus Polynesian introductions does not show a significant difference in growth forms ($\chi^2 = 7.48$, df = 4, $P = .112$), in this case affirming the null hypothesis of no substantial change in the array of growth forms between endemic and indigenous species and Polyne-
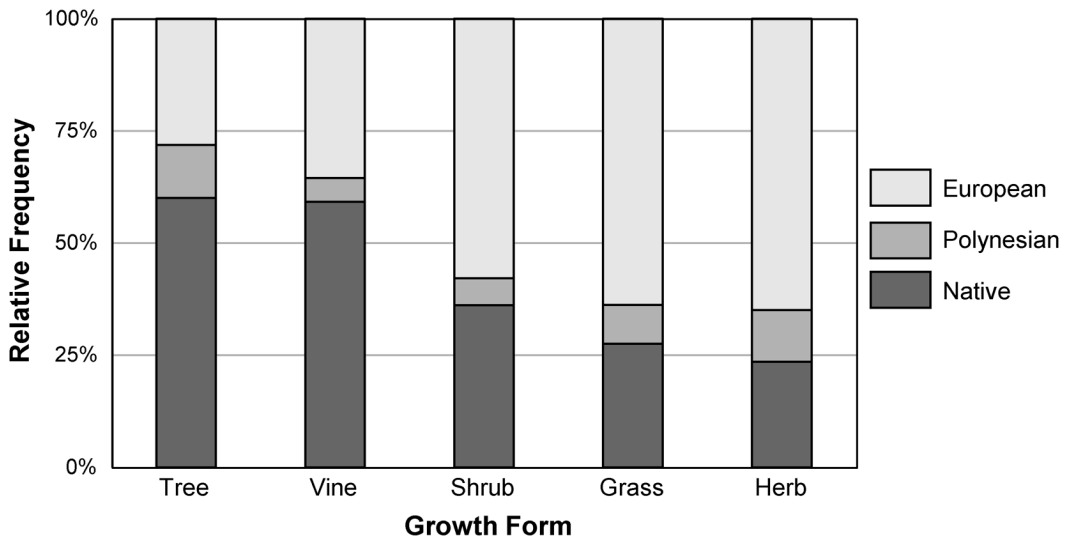
FIGURE 2. Relative frequency of plant species by growth form for each origin type: endemic and indigenous species, Polynesian introductions, and European introductions. Total plant species in each category: trees ($n = 213$), vines ($n = 76$), shrubs ($n = 83$), grasses ($n = 58$), and herbs ($n = 174$).

sian species. Therefore, although the growth forms of Polynesian plants closely resemble those of endemic and indigenous species, the mix of growth forms among European introductions represents a substantial departure from previously introduced vegetation.

The overstory plants of Tonga, consisting largely of native or Polynesian introduced trees, contrast markedly with the understory (grasses, herbs, and shrubs), which includes species more indicative of culturally modified vegetation, introduced largely after European contact (Figure 2). Trees are most commonly endemic or indigenous to the islands, whereas grasses, herbs, and shrubs tend to be post-European contact introductions. Polynesian introductions are mainly trees (25 taxa) and herbs (20 taxa). A staggering 175 of the 232 graminoid and herbaceous taxa are introduced, whereas only 85 of the 213 tree taxa are introductions.

Among abiotic dispersal mechanisms, all growth forms, except herbs, are dispersed more commonly by water than by wind (Table 3). The native flora, which includes the majority of tree and vine taxa, is characterized by internal animal dispersal, primarily by birds; comparable frequencies of wind versus water dispersal; and very low incidence of dispersal by human cultivation. Adventive Polynesian introductions (mostly trees or herbs) feature bird dispersal and endozoochory, dispersal by water more commonly than wind, and the highest frequencies of dispersal by bats and rats, or by intentional human cultivation (e.g., breadfruit). European introductions (primarily graminoids, herbs, and shrub taxa) characteristically are dispersed by endozoochory and birds but also reveal the highest frequency of external animal dispersal and the lowest proportion of bat dispersal.

DISCUSSION

This study investigated plant dispersal patterns to elucidate millennial- to century-length changes in the ecology of tropical rain forests on the islands of Tonga in the South Pacific. The ecological history of Tonga is marked by multiple introductions of new plants, animals, and human populations, each leading to disrupted plant dispersal guilds and attendant ecological impacts. The native flora and fauna of Tonga have been subjected to

TABLE 3

Number of Tongan Plant Species Dispersed by Each Mechanism and Percentage (%) of the Total Number of Species (*n* Species) in Each Growth Form

Growth Form	Dispersal Mechanism								
	Water	Wind	Internal	External	Bat	Bird	Rodent	Hum Cult	*n* Species
Tree	103 (48%)	35 (16%)	173 (81%)	11 (5%)	108 (51%)	171 (80%)	34 (16%)	68 (32%)	213
Vine	35 (46%)	8 (11%)	45 (59%)	1 (1%)	26 (34%)	46 (61%)	0 (0%)	19 (25%)	76
Shrub	36 (43%)	17 (20%)	45 (54%)	22 (27%)	9 (11%)	53 (64%)	7 (8%)	32 (39%)	83
Herb	72 (41%)	80 (46%)	73 (42%)	64 (37%)	4 (2%)	84 (48%)	8 (5%)	61 (35%)	174
Grass	34 (59%)	22 (38%)	29 (50%)	38 (66%)	0 (0%)	33 (57%)	1 (2%)	5 (9%)	58

Note: Dispersal mechanisms include water; wind; internal animal dispersal (Internal); external animal dispersal through adhesion (External); dispersal involving bats, birds, and rodents; and human cultivation (Hum Cult). For example, 34 (59%) of grasses are dispersed by water. Because the taxa within a growth form may be dispersed by more than one mechanism, the relative frequencies for each growth form total more than 100%.

spatial and temporal perturbations through a variety of natural (tropical cyclones) (Woodroffe 1983, Franklin et al. 2004, McConkey et al. 2004) and human-caused disturbances (fire, deforestation, and predation) (e.g., Steadman 1995, 2006, Fall 2005). On Tongatapu, native rain forest species persist only in small patches (Palmer 1988, Wiser et al. 2002). In contrast, greater expanses of native rain forests are found on the larger islands of ʻEua and Vavaʻu, where they also have been thinned or mixed with forest plantations (e.g., Whistler 1992*b*, Drake et al. 1996, Franklin et al. 1999). Howe and Miriti (2004) pointed out the importance of studying dispersal systematically in cases of ecological disruption where forests have become fragmented and some dispersal vectors have been lost. Chronic stress on indigenous plant species involves loss of native animals, especially fruit-eating birds and bats. In tropical regions where overhunting has removed animal dispersers, forest communities may change dramatically over a mere 20- to 30-yr time scale (Howe and Miriti 2004). Starting about 3,000 yr ago, Tonga has lost about half of its land birds (Steadman 1995, 2006) and one of the islands' flying foxes (Koopman and Steadman 1995). Three additional frugivores, the Friendly Ground-Dove (*Gallicolumba stairi*), the Many-Colored Fruit-Dove (*Ptilinopus perousii*), and the Blue-Crowned Lorikeet (*Vini australis*), are endangered or have been extirpated from the main islands in the last 150 yr (Steadman and Freifeld 1999). The loss of these key dispersers has imperiled the recruitment of trees with the largest seeds or fruits (Meehan et al. 2002, McConkey and Drake 2006, 2007). Ecological disruptions emerge clearly in rain forests where fragmentation diminishes populations of fruit-eating birds, bats, and primates (Cordeiro and Howe 2003, Babweteera and Brown 2010, Melo et al. 2010) and impedes forest regeneration (Silva and Tabarelli 2000, Cordeiro and Howe 2001, Stoner et al. 2007).

Seed dispersal is one of the key factors in understanding ecological patterns and processes throughout the world (van der Pijl 1982). In particular, animals are recognized for their importance as dispersal vectors in tropical environments (e.g., Gentry 1982,

Howe and Smallwood 1982). Accordingly, our data highlight the importance of animal dispersal for most of the plant species in Tonga. Bird and endozoochorous dispersal are well represented across all categories in our data, in keeping with other studies showing that animal dispersal (usually internally) dominates most ecosystems worldwide (Howe and Smallwood 1982) and is particularly critical on tropical islands (Whittaker and Jones 1994). Islands incorporate less ecological partitioning among vertebrate dispersers than is found in continental ecosystems, where numerous frugivores may be available to disperse rain forest trees. For example, no fewer than 39 vertebrate dispersal agents were identified in a tropical forest in Gabon (Gautier-Hion et al. 1985). On islands where bats are the only mammals (other than subsequently introduced rats) there is necessarily less niche specialization. With the introduction of rats to island ecosystems like Tonga, considerable dispersal overlap develops among birds, bats, and rats, particularly with seed predation by rats (Louda and Zedler 1985, Abe 2007). Predispersal predation impacts species with dry fibrous drupes disproportionately more than tree species with brightly colored berries or drupes (Gautier-Hion et al. 1985). Although herbivory and seed predation are thought to be relatively less important on islands than on mainlands (e.g., Carlquist 1974), predation represents a serious impediment to seed survival and seedling recruitment (Abe 2007, Meyer and Butaud 2009). Our data demonstrate that seed predation by rats may inhibit dispersal among native rain forest trees in particular. Thus, predispersal rodent predation, well documented on Pacific islands (e.g., McConkey et al. 2003, Meyer and Butaud 2009, Prebble and Wilmshurst 2009), has pervasive ecological implications for the continued regeneration of native rain forest species.

Fruit bats are crucially important seed dispersers in many tropical ecosystems (Banack 1998, Muscarella and Fleming 2007). In particular, dispersal by bats, either internally or by grasping with their claws, is very important for the propagation of trees and vines (which tend to be indigenous or endemic), but bats rarely disperse understory plants (which are often introduced). Strikingly, our data show that dispersal by the Tongan fruit bat (*Pteropus tonganus*) is twice as common among native and Polynesian plants as among European introductions, underscoring the importance of these animals for the dispersal of native plant species, in contrast to their notable lack of assistance to nonnatives. Fruit bat populations are declining on many Pacific islands, often due to hunting (Rainey et al. 1995, Banack 1998). In Tonga they are the protected property of the King in the village of Kolovai on Tongatapu (Grant 1998). However, fruit bat populations in Samoa and Tonga have been slashed repeatedly (up to 80%–96%) due to cyclone winds or hunting and starvation following defoliation in the wake of cyclones (Craig et al. 1994, Pierson et al. 1996, McConkey et al. 2004). This suite of factors works to further diminish bats' selective dispersal of primarily native and Polynesian species (see, for example, Nelson et al. 2000*a,b*, Luskin 2010). Thus, bats emerge as acutely vulnerable, yet particularly crucial, plant dispersers for pre-European contact plants in the Tongan ecosystem.

Because the majority of trees and vines are indigenous and endemic species, this overstory provides the strongest reflection of vegetation before human arrival on Tonga. The original colonists of Polynesia introduced a wide array of domestic animals and plants (e.g., Kennedy and Clarke 2004). Walter and Sam (2002) stressed the antiquity and importance of arboriculture in Oceania, in particular. Our data suggest that the populations that arrived in Tonga 3,000 yr ago cultivated only a few native plant species but brought with them a suite of domesticates as canoe plants from Melanesia. In the more remote oceanic islands, including Tonga, Polynesians introduced herbaceous cultigens, particularly root crops and trees for fruits, nuts, and building materials (Whistler 1991). On Tonga, fossil evidence reveals the introduction of *Cordyline fruticosa* and *Pometia pinnata*, as well as the cultivation of indigenous *Pandanus tectorius*, *Cocos nucifera*, *Casuarina equisetifolia*, and *Canarium harveyi*, all taxa that expanded after Polynesian settlement (Fall 2010). It is

possible that a new variety of coconut was introduced by Polynesian settlers; however, based on pollen analysis it is impossible to separate different varieties of *Cocos nucifera*. Prebble (2008) found that *Aleurites moluccana*, *Broussonetia papyrifera*, *Cocos nucifera*, and *Cordyline fruticosa* were introduced as cultivated trees or shrubs on many subtropical islands in the South Pacific. This transportation and cultivation of woody species into remote Oceania stands in contrast to the extensive utilization of rain forest species, including many species of *Pandanus*, palms, and tropical hardwoods, in the Indo-Malayan peninsula and in Melanesia (Barrau 1963, Yen 1974, Denham et al. 2003). Similarly, most of the herbaceous Polynesian cultigens found in Tonga are derived from Melanesia or Southeast Asia. Polynesians introduced herbs, *Alocasia macrorrhizos*, *Colocasia esculenta*, and *Ipomoea batatas*, and a cultivated grass, *Saccharum officinarum*, to Tonga and other South Pacific islands (Prebble 2008, Fall 2010).

The importance of species origins, source areas, and residence time in an ecosystem is critical to predicting and explaining plant invasions (Pyšek et al. 2004). Our results support the inference that the overstory and understory were influenced differentially by the successive introductions of plants through Polynesian colonization and following European contact. Polynesian introductions originate in similar tropical environments in Melanesia or Indonesia, whereas understory species more often are weedy or early successional species (e.g., Fall et al. 2007) and originate in very different subtropical or temperate environments. As a case in point, among European introductions and understory taxa, external animal dispersal is twice as common as bat dispersal. Wind-dispersed species also tend to be early successional and poorly represented in forest understory environments, because the forest itself creates a barrier to wind that impedes subcanopy wind speeds and, thereby, the propagation of these species (Gentry 1982, Howe and Smallwood 1982). Long-term thinning of rain forests, beginning 3,000 yr ago (Fall 2005), to more open coconut plantations and other agricultural lands (Whistler 1992*b*, Drake et al. 1996, Franklin

et al. 1999) reduces this natural windbreak effect, subsequently promoting the establishment of wind-dispersed understory species. In addition, thinning of the rain forest on Tonga may have reduced plant species with larger seeds that are animal dispersed and more shade tolerant (Meehan et al. 2002, McConkey et al. 2004).

We tested and rejected the null hypothesis that human introduction of plant and animal species would not change the proportional representation of dispersal guilds. Accordingly, although the indigenous and endemic flora of Tonga is overwhelmingly bird, bat, and water dispersed, the addition of human-cultivated or -dispersed species has shifted the flora toward an increase in understory species and nonnative, externally animal-dispersed taxa. Plants introduced after European colonization often are wind and epizoochorously dispersed (largely early successional or weedy species) and do not benefit from bat dispersal, which selectively favors native species. Furthermore, the loss of the Samoan fruit bat and several of the largest frugivores following Polynesian colonization, subsequent introduction of rats and exotic birds, and additional loss of native fauna after European contact (Steadman 2006) has disrupted dispersal guilds on Tonga. Key ecological implications of human colonization in Tonga include (1) the introduction and cultivation of nonnative plant species; (2) the introduction of new fauna, such as rats, that prey disproportionately on native plant species, particularly indigenous rain forest trees and vines; and (3) the thinning of forests, which encourages the establishment of nonnative, weedy, early successional species at the expense of native species. Further impacts involve the decimation of bat populations that are key dispersers of native plant species. These systematic changes in dispersal guilds reveal a suite of crucial implications for the dynamics and sustainability of the Tongan ecosystem.

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