Species Origins, Dispersal, and Island Vegetation Dynamics in the South Pacific

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We characterize the vegetation of the Kingdom of Tonga, South Pacific, by exploring the effects of species–area relationships, species isolation, and long-distance dispersal. Published literature provides data for eleven main islands of Tonga on species richness, vegetation types, origins, and dispersal mechanisms. Island area, maximum elevation, distance from neighboring archipelagos, and island geology provide key variables with which to consider the configuration of Tonga's floral biodiversity. Vegetation communities are evaluated by dispersal mechanisms, species origins, and island age as reflected by geology. Species–area relationships are significant for all plant species and for ancient and modern introductions, and species richness shows significant relationships to maximum elevation for indigenous plants and modern introductions. In contrast, species richness on the islands of Tonga does not correspond to patterns expected for species–isolation relationships with the nearest archipelagos of Samoa and Fiji. Plant dispersal spectra vary significantly according to island topography, geology, vegetation types, and plant species origins. The youngest volcanic islands have the most wind-dispersed species, whereas the older limestone islands have more bird, water, and human-dispersed plants. Tongatapu, the largest and longest inhabited island, reflects the legacy of a deeply humanized landscape where more than half the plants are introduced. In contrast, on the sparsely populated, more remote islands, and in many vegetation types, 70 to 90 percent of the plants are native. Evidence for species introductions, varying impacts on different vegetation types, and associated changes in dispersal spectra reveal key aspects of biogeographic dynamics in Tonga and potentially for island biogeography elsewhere. *Key Words: long-distance dispersal, plant species origins, South Pacific islands of Tonga, species–area relationships, species–isolation relationships.*

我们透过探讨物种—面积关系、物种隔离, 以及长距离散布的影响, 描绘南太平洋东加王国的植物特徵。出版文献提供了东加十一座主要岛屿的物种丰富性、植物种类、起源与散布机制的资料。岛屿面积、最高海拔、与周围列岛的距离, 以及岛屿的地质, 皆提供做为考量东加的植物生物多样性形态的主要变因。植物群落透过散布机制、物种起源, 以及由地质学所反映出的岛屿年龄来评估。对所有的植物物种以及古老与现代的引入植物而言, 物种—面积关系皆非常显着, 而对原生植物和新引入植物而言, 物种的丰富性与最高海拔呈现出显着关系。相对而言, 东加群岛上的物种丰富性, 与最为邻近的萨摩亚与斐济群岛上所预期的物种—隔离关系模式并不相符。植物散布的光谱, 随着岛屿的地形、地质、植物种类和植物物种起源, 而有着显着的差异。较为年轻的火山岛屿拥有最多的风散播物种, 而较为古老的石灰岩岛屿则有着较多的鸟、水, 以及人类散布的植物。东加塔普, 东加最大以及最长的人类定居岛屿, 反映了深刻的人类化地景遗迹, 其中半数以上的植物皆为外来引进的。反之, 在鲜少人定居、较为偏远的岛屿上, 以及在许多植物类型中, 百分之七十至九十的植物皆是原生的。物种引进的证据、对不同植物类型的不同影响、以及散布光谱的相关改变, 揭露了东加的生物地理动态以及可能是其他岛屿生物地理学的重要面向。 *关键词: 长距离散布, 植物物种起源, 南太平洋东加群岛, 物种—面积关系, 物种—隔离关系。*

Para caracterizar la vegetación del Reino de Tonga, en el Pacífico Sur, exploramos los efectos de las relaciones especie–área, el aislamiento de las especies y la dispersión a gran distancia. En la literatura disponible se encuentran datos de once de las principales islas de Tonga sobre riqueza de especies, tipos de vegetación, orígenes y mecanismos de dispersión. El área de la isla, la altura máxima, la distancia a los archipiélagos vecinos y la geología isleña actúan como las variables claves a partir de las cuales considerar la configuración de la biodiversidad floral de Tonga. Las comunidades vegetales son evaluadas contra los mecanismos de dispersión, orígenes de las especies y la edad de las islas reflejada en su geología. Las relaciones especie–área son significativas para todas las especies de plantas y para introducciones antiguas y modernas, y la riqueza en especies muestra relaciones significativas con la altura máxima en lo que concierne a plantas indígenas e introducciones modernas. Por contraste, la riqueza de especies en las islas de Tonga no tiene correspondencia con los patrones esperados para las relaciones

especie–aislamiento con los archipiélagos más cercanos de Samoa y Fiji. Los espectros de dispersión de plantas varían significativamente según la topografía, geología, tipos de vegetación y origen de las especies vegetales de las islas. Las islas volcánicas de menor edad tienen las especies más caracterizadas por su dispersión eólica, mientras que las islas calizas más viejas tienen más especies cuya dispersión se debe a aves, al agua o al hombre. Tongatapu, la isla más grande y de más antiguo poblamiento, refleja el legado de un paisaje profundamente humanizado, registrando más de la mitad de sus plantas como importadas. Por contraste, en las islas más remotas y débilmente pobladas, y en muchos tipos de vegetación, entre el 70 y el 90 por ciento de las plantas son nativas. La evidencia de introducciones de especies, los variable impactos sobre diferentes tipos de vegetación y los cambios asociados en diferentes espectros de dispersión, revelan aspectos claves de la dinámica biogeográfica de Tonga, lo mismo que, potencialmente, de la biogeografía isleña en otros contextos insulares. *Palabras clave: dispersión a gran distancia, orígenes de especies vegetales, islas sur pacíficas de Tonga, relaciones especies–áreas, relaciones especies–asilamiento.*

This article explores plant species patterns on the remote oceanic islands of the Kingdom of Tonga. We investigate the interaction of the species–area relationship, species–isolation influences, and long-distance dispersal to explain current vegetation patterns by considering species origins, island geology, vegetation types, and a wide range of plant dispersal vectors. We test three interrelated hypotheses: (1) The vegetation patterns of Tonga adhere to the basic principles of the species–area relationship (Lomolino, Riddle, and Brown 2006), as a surrogate for habitat diversity (Ricklefs and Lovette 1999) and a reflection of the archipelago's vegetation history (especially involving introductions of new plant species); (2) vegetation diversity among the islands of Tonga and between this archipelago and neighboring island groups will reveal interisland biogeographic relationships based on isolation, long-distance dispersal, and geological similarities with potential source areas; and (3) the incorporation of plant dispersal data with vegetation type, geology, and plant origins will demonstrate that Tongan biogeographic change is heavily predicated on the effects of plant and animal introductions and human behavior on the plant dispersal spectra of Tonga.

MacArthur and Wilson's (1967) equilibrium model has revitalized modern biogeography by providing a theoretical framework within which to explain patterns of species richness and biological diversity on islands. The species–area relationship remains influential due to its consistency and applicability to a wide array of environmental settings and organisms (e.g., Heaney 2007; Whittaker and Fernandez-Palacios 2007; Triantis et al. 2008; Whittaker, Triantis, and Ladle 2008; Stracey and Pimm 2009; Diver 2010; Losos and Ricklefs 2010; Lyons et al. 2010). Triantis et al. (2008) noted that prediction of island biodiversity based on the species–area relationship is improved by incorporating additional variables such as island age, isolation, or environmental heterogeneity. Accordingly, island species–area relationships

are conditioned by the variety of available habitats, climatic variability, and elevation range (Price and Wagner 2011). Thus, the composition and species richness of terrestrial biotas on the islands of Tonga might reflect not only the species–area relationship but also distance to source areas (in this case Southeast Asia or the nearer islands of Fiji and Samoa as stepping stones), island age, elevation, and environmental variables such as soil and geology.

Island biodiversity also is conditioned by the interplay of these variables with systems of plant dispersal. The study of plant dispersal lies at the heart of biogeography, given that dispersal is the basic ecological process that reflects the adaptation of each plant species for the movement of seeds or other diaspores (hereafter seeds) from its source plant to its successful establishment in a location suitable for reproduction. Most instances of dispersal involve distribution of seeds over relatively short distances, thereby contributing an important molding influence on the configuration of localized plant communities. Thus, dispersal studies have recognized the importance of relatively frequent "specialized dispersal" of a plant taxon through a standard vector determined by seed morphology (Berg 1983; Higgins, Nathan, and Cain 2003).

Dispersal studies also recognize the importance of long-distance dispersal (LDD) as a formative influence on large-scale biogeographic phenomena (Gillespie et al. 2011). LDD syndromes can be defined in several ways; for example, on the basis of a distance threshold (e.g., >100 m; Cain, Milligan, and Strand 2000) or a fraction of 1 percent of all seeds having a mean dispersal distance of 500 m (Higgins and Cain 2002). However defined, LDD extends to transoceanic distances (Nathan 2006), a phenomenon exemplified particularly well among Pacific islands. Thus, interisland dispersal in an archipelago such as Tonga qualifies as long distance. LDD is characterized by rare or "extreme" events, which are nonetheless disproportionately

important in influencing a variety of ecological processes that mold island plant ecology. In addition to relatively unpredictable natural phenomena, such as severe meteorological episodes, "human-mediated LDD can be considered an extreme event" (Nathan 2006, 787). Thus, LDD emerges as a central element in island biodynamics (Gillespie et al. 2011). Yet, LDD research is hampered by data that might be limited to a specific taxon or dispersal patterns bounded at a maximum of a few hundred meters. Further, although seed morphology could be interpreted to indicate a single "standard" dispersal vector, plants tend to be dispersed by multiple vectors, such that the influences of each vector will vary over differing geographical settings and scales (Myers et al. 2004; Couvreur et al. 2005; Spiegel and Nathan 2007). Generalized dispersal often also involves a suite of nonstandard vectors (Berg 1983). Accordingly, recent studies emphasize the importance of dispersal by multiple vectors (Ozinga et al. 2004; Jordano et al. 2007; Nathan 2007; Nathan et al. 2008).

This study assesses the vegetation of Tonga based on the effects of plant dispersal, especially LDD, and a suite of environmental variables that influence vegetation dynamics in the archipelago. In this context, LDD is a crucial ecological component of island colonization (Carlquist 1974). Although humans might be consid-

ered a generalized LDD vector in light of current global human-induced ecological changes, the colonization of Tonga, first by Polynesians and subsequently by Europeans, involved more specific disjunctions in plant ecology over differing timescales and involving differing suites of dispersal vectors. Thus, the historical biogeography of Tonga provides an ideal perspective with which to evaluate the evolving interactions of island plant ecology.

Study Area

The Tongan archipelago includes more than 170 islands, which make up the Tongatapu, Ha'apai, Vava'u, and Niuatoputapu island groups (Figure 1). The Kingdom of Tonga incorporates about 700 km^2 of land spread over approximately 600,000 km^2 of the southern Pacific Ocean between 23° and 15°S, and 173° and 177°W. A tropical maritime climate is dominated by the southeasterly trade winds for most of the year, with mean annual precipitation increasing from south to north and ranging from 1,780 mm on Tongatapu to 2,340 mm in Vava'u (Thompson 1986). Tonga is one of the most active seismic and volcanic areas on earth, creating a particularly dynamic setting for the study of island
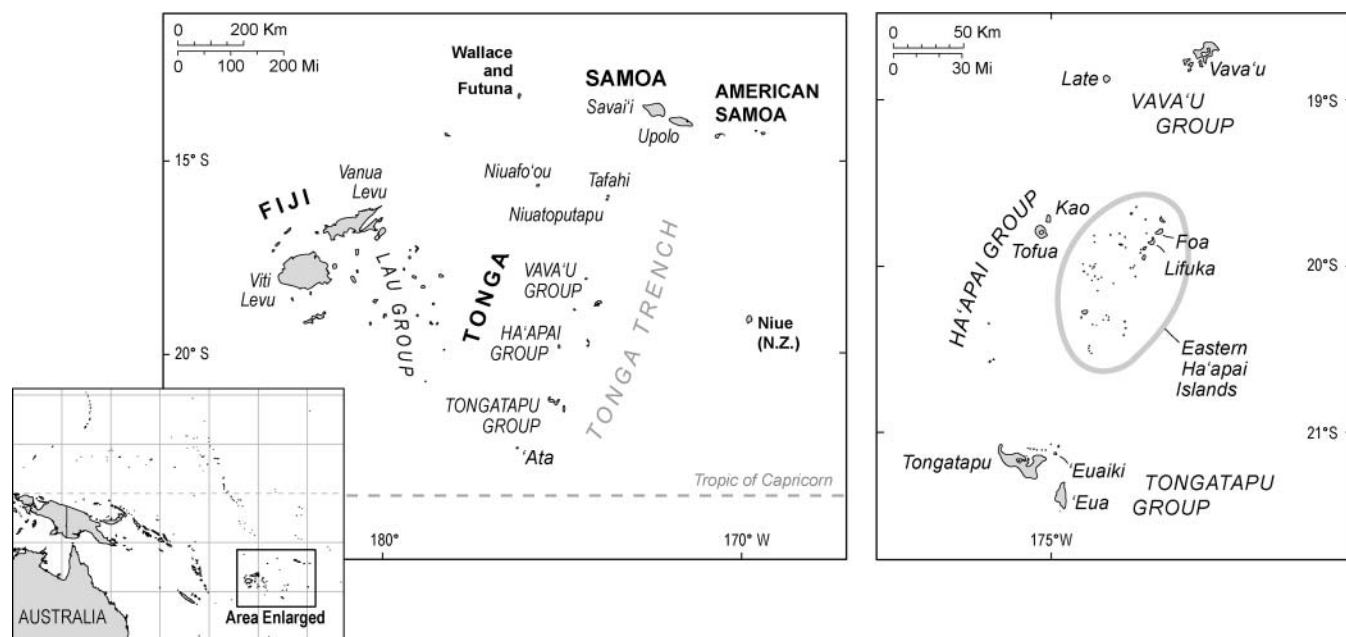
Figure 1. Location of the Kingdom of Tonga in the south Pacific Ocean. Left: The position of Tonga relative to the larger islands of Fiji and Samoa and the location of Tonga's northernmost islands (Niuafo'ou, Tafahi, and Niuatoputapu; inset showing location in South Pacific). Right: The main three island groups of Tonga, the Vava'u, Ha'apai, and Tongatapu island groups. Eastern Ha'apai Islands refers to the limestone islands of the Ha'apai group, as distinct from the volcanic islands of Kao and Tofua. In this article, vegetation data for E. Ha'apai pertain only to the two main limestone islands of Foa and Lifuka that are joined by a causeway.

Table 1. Islands in the Kingdom of Tonga with vegetation data listed by island size

Island	Island group	Area (km²)	Elevation (m)	Island type (age or date last erupted)	Plants (n)	Population[a] (2006)
Tongatapu	Tongatapu	261	80	Uplifted limestone (1–10 mya)	390	72,045
Vava'u	Vava'u	119	200	Uplifted limestone (1–10 mya)	251	15,505
'Eua[b]	Tongatapu	81	312	Uplifted limestone (1–10 mya)	335	5,206
Niuafou'ou	Niuatoputapu	52.3	205	Shield volcano (1985)	100	646
Tofua[c]	Ha'apai	47	558	Caldera volcano (1959)	248	0
Late[d]	Vava'u	17.4	519	Stratovolcano (1854)	196	0
E. Ha'apai[e]	Ha'apai	17	60	Uplifted limestone (1–10 mya)	103	7,570
Niuatoputapu	Niuatoputapu	15.6	146	Volcanic w/ limestone reef (3 mya)	222	950
Kao[c]	Ha'apai	13	1,046	Stratovolcano (historic)	192	0
Tafahi	Niuatoputapu	3.4	506	Stratovolcano (Holocene?)	66	69
'Euaiki	Tongatapu	1	40	Uplifted limestone (1–10 mya)	62	0
Kingdom of Tonga (total population)						101,991

[a]Kingdom of Tonga Department of Statistics (2008, Table G1).
[b]'Eua has both limestone and volcanic rocks.
[c]Historic population estimates are about 200 people on Tofua and Kao; following the eruption of Tofua in 1959 the Tongan government relocated the people of Tofua and Kao.
[d]Historic population estimates are about 350 people on Late; Late last erupted in 1854; people relocated in late 1880s to other islands.
[e]Vegetation data for E. Ha'apai pertain to the two main limestone islands of Foa and Lifuka that are connected by a causeway.

vegetation. Periodic volcanic eruptions would have destroyed entire island biotas during the Holocene and historic past, simultaneously enriching soils with ash fall. The volcanic islands are younger (still forming in some cases), higher in elevation, and less densely populated than their limestone counterparts (Table 1). The uplifted limestone islands are older, lower in elevation, have relatively rich soils (large portions of which are under cultivation), and have the greatest population densities. The geological and age differences between the limestone (1–10 millions of years) and recent volcanic islands of Tonga create variable settings for island biotas, human colonization and settlement, and vegetation change.

The Kingdom of Tonga is part of the Western Polynesian biogeographic subregion (Mueller-Dombois and Fosberg 1998) of the southwestern Pacific, and its position holds basic implications for its biological affinities and diversity. Tonga lies about 320 km east of the Lau island group of Fiji and 260 km south of Savai'i in the Samoan archipelago (as measured from the northernmost Tongan island, Tafahi). Accordingly, the plants of Tonga are most similar to the flora of Fiji (Smith 1979–1991) and Samoa (Whistler 1992b, 2002). The kingdom is situated at the eastern edge of the Indo-Malesian floral realm (van Steenis 1979) in which floral impoverishment increases with distance from tropical Southeast Asia and the islands of Melanesia. For example, Tonga marks the eastern limit of cycads (Hill 1996)

and conifers (de Laubenfels 1996); Tonga and Samoa bound the eastern distribution of mangroves on Pacific islands (Whistler 1992b). Park and Whistler (2001) estimated that 450 indigenous plants grow on Tonga, whereas the larger, higher, and more diverse islands of Samoa contain about 550 species of angiosperms, plus 215 fern species (Whistler 1992b). The addition of nonnative species roughly doubles the number of plant species on Tonga (Fall and Drezner 2011). Over 70 percent of Tongan plant species also grow on Samoa, where endemics constitute about 30 percent of the plant species, in contrast to only 3 percent in Tonga (Whistler 1992b). Thus, the greater isolation of Tonga from plant source areas in Melanesia and Southeast Asia suggests an explanation for its more impoverished flora.

The vegetation of Tonga can be divided into eight broad categories: (1) mangroves, coastal swamps, or wetlands; (2) littoral strand or scrub; (3) littoral forest; (4) *Casuarina* forest; (5) lowland rain forest; (6) secondary rain forest; (7) upland rain forest; and (8) volcanic vegetation (including fern lands; Whistler 1992b; Mueller-Dombois and Fosberg 1998). Coastal swamps, wetlands, and mangrove vegetation are limited to limestone islands (Ellison 1989; Crane 1992). Coastal marshes, found on the limestone islands of Tongatapu, Vava'u, and Ha'apai, often are used for taro cultivation where weedy species, such as *Polygonum* cf. *glabrum, Ludwigia octovalvis,* and grasses (*Paspalum conjugatum*) now dominate (Whistler 1992b). The upper

elevations of Tonga's highest volcanoes are treeless fern lands. In the Tongan archipelago, only 'Eua has well-developed lowland and upland rain forest communities.

Tonga has a total population of slightly more than 100,000 people (Kingdom of Tonga Department of Statistics 2008; see Table 1) spread over about 21 percent of the Tongan islands (Park and Whistler 2001), but many outer islands are losing occupants. The largest island, Tongatapu, is heavily cultivated and has the highest population density in Tonga, with about 70 percent of the nation's inhabitants (Kingdom of Tonga Department of Statistics 2008). The central island group, Ha'apai, consists of many small low limestone islands, where most of its 7,570 inhabitants live, with maximum elevations up to 60 m and reefs (referred to as eastern Ha'apai), and a string of five volcanic islands to the west, including the larger islands of Kao and Tofua. The only inhabited volcanic island in Ha'apai, Tofua, has two small villages that are occupied only by seasonal residents tending gardens and kava plantations (Park and Whistler 2001). Tofua, an active volcano with a long history of eruptions, was erupting when James Cook visited in 1774 on his second voyage and again when Captain William Bligh and eighteen loyal crewmen from the *Bounty* were set adrift near the island in 1789. In 1854 Tofua was evacuated, it experienced a major eruption in 1959, and molten lava was observed in its crater in 2009 (Smithsonian Institution National Museum of Natural History Global Volcanism Program 2013). The nearby island of Kao, a strato-volcano, reaches an elevation of 1,046 m, the highest point in Tonga.

The limestone islands of the Vava'u island group, inhabited by more than 15,505 people, include outlying active volcanic islands. Fonualei and Late last erupted in 1846 and 1854, respectively, and Late'iki alternately exists as an island or a submarine seamount. At the northern limit of Tonga, Niuatoputapu, an ancient eroded volcanic island surrounded by a limestone reef, had a population of 950 people in 2006. Tafahi, a stratovolcano inactive in the historic past, had only sixty-nine occupants in 2006. Both islands show a population decline of 37 percent over the past twenty years. Niuafo'ou, the only volcanic island in Tonga not on the Tofua arc, is a shield volcano formed along the Lau spreading center, which last erupted in 1985. Due to the numerous volcanic eruptions and the destruction of many villages in the past century, the people of Niuafo'ou were resettled on 'Eua in 1947. Of special note, the shores of the island's active volcanic crater lake are home to the endemic Niuafo'ou megapode, the only remaining megapode in Tonga (Steadman 2006).

The human colonization of Tonga began on the largest island of Tongatapu. The Nukuleka site, dated to 2900–2850 cal BP, is the founder settlement, not only for Tonga but for the whole of Polynesia (Burley and Dickinson 2001, 2010). Based on Lapita ceramic motifs and tempers, the first Tongan people arrived on Tongatapu from central Melanesia in a leapfrog migration that bypassed Fiji, which had been settled about a century earlier (Burley and Dickinson 2001, 2010). The Polynesian settlement of Tonga engendered a suite of ecological changes to the indigenous and endemic biota (Fall 2005). Previously, rain forest vegetation would have covered virtually all of the inland landscapes of Tonga, except in wetlands and areas of recent volcanism with poor soil development (Wiser et al. 2002). Much of this original forest has been cleared or transformed into secondary rain forest through human intervention. Along with the wholesale transformation of the landscape through forest clearing and burning, Lapita people also brought a suite of trees (e.g., *Canarium harveyi* and *Pometia pinnata*) and herbaceous cultigens (including *Colocasia esculenta* and *Ipomoea batatas*; Fall 2010).

The impacts of human colonization had similarly profound implications for animal species and their roles in plant dispersal. Polynesian colonization resulted in the extirpation of one of the two native seed-dispersing fruit bats, the Samoan flying fox (*Pteropus samoensis*; Koopman and Steadman 1995). Although the Tongan fruit bat (*Pteropus tonganus*) occupies most islands in Tonga today, it might play a diminishing role in plant dispersal as its populations decline (Meehan, McConkey, and Drake 2002; McConkey and Drake 2006, 2007). Polynesian settlers introduced the domestic pig (*Sus scrofa*) and the Polynesian rat (*Rattus exulans*; Twibell 1973; Dye and Steadman 1990), leading directly or indirectly to the extinction of numerous land birds (see Steadman 1995, 1998, 2006). European animal introductions include the ship rat (*Rattus rattus*), which is a seed predator in tropical forests that disrupts rain forest regeneration (McConkey et al. 2003; Meyer and Butaud 2009; Prebble and Wilmshurst 2009).

Materials and Methods

This study works from a compendium of 796 plant species compiled from a variety of published sources on the vegetation (as there is no complete flora) of Tonga (Hemsley 1894; Burkill 1901; Yuncker 1959; Uhe 1974; Sykes 1978, 1981; Palmer 1988; Ellison 1990; Whistler 1991, 1992a, 1992b, 1995; Crane 1992;

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 et al. 2006). Plant nomenclature follows Smith (1979–1991) and Whistler (1991, 1992a, 1992b, 1995). Our presence-only data for each plant species includes the Tongan islands on which it is found, the vegetation communities or types in which it occurs, its origin on Tonga, and its mechanisms for seed dispersal. A previous study of dispersal ecology in the lowland rain forest of Vava'u presents the raw data for 125 plant species (Fall, Drezner, and Franklin 2007). Subsequent research (Fall and Drezner 2011) incorporates the full data set for 796 species on the entire Tonga archipelago by investigating overstory and understory vegetation growth forms according to dispersal vectors and species origins. This article presents island-specific data by considering vegetation biodiversity, species origins, island geology, vegetation types, and plant dispersal vectors on eleven islands and eight vegetation communities to address the basic tenets of island biogeography as exemplified in the archipelago of Tonga.

The islands of Tonga vary in area, maximum elevation, geological type, and modern population (Table 1). Island sizes are reported in Whistler (1992b), Park and Whistler (2001), Franklin et al. (2006), and the UN System-Wide Earthwatch (1998). Dickinson and Burley (2007) provide estimated ages for the uplifted limestone islands of Tongatapu, 'Eua, Ha'apai, and Vava'u, ranging from 1 to 10 million years. The volcanic island chain of Tonga is still active, with eruptions as recent as 2009. Further information on island age, volcanic eruption history, and volcano type is derived from the Smithsonian Institution National Museum of Natural History Global Volcanism Program (2013). We present our analyses in a series of steps that consider island characteristics, dispersal mechanisms, and species origins.

We evaluated the origin of every plant species in Tonga; if there were discrepancies for the origin of a species between sources we omitted that species from our analysis (Table 2). Species origins for Tonga were classified as endemic, indigenous, Polynesian introduction, or European introduction, as determined primarily by Whistler (1991, 1992a, 1992b, 1995). Because there is no complete flora of Tonga, additional sources were used to classify plant origins, identifying endemic and indigenous taxa, those of Polynesian origins and later postcontact European plant species (e.g., Smith 1979–1991; Sohmer and Gustafson 1987; Wagner, Herbst, and Sohmer 1999; Wagner and Lorence 2002;

Table 2. Number of plant species by origin for each of the major Tongan islands shown for both limestone and volcanic islands (listed by descending island area)

	n	Endemic and indigenous	Polynesian	European
Limestone islands				
Tongatapu	345	142	39	164
Vava'u	225	155	23	47
'Eua	311	241	25	45
E. Haapai[a]	93	59	15	19
'Euaiki	52	28	6	18
Volcanic islands				
Niuafo'ou	89	55	5	29
Tofua	229	162	19	48
Late	154	120	15	19
Niuatoputapu	170	84	29	57
Kao	172	139	11	22
Tafahi	56	43	8	5

Note: Percentage data are shown in Figure 5. Chi-square test of origin type versus island (without Tafahi and 'Euaiki): $\chi^2 = 393.85$, minimum expected value $= 17.06$, $df = 16$, $p = 7.1 \times 10^{-74}$.
[a]Vegetation data for E. Ha'apai pertain to the two main limestone islands of Foa and Lifuka that are connected by a causeway.

Prebble 2008; Price and Wagner 2011). As there are few endemic species on Tonga (<3 percent of the flora), we combine indigenous and endemic species into one category to represent the native or prehuman vegetation. Polynesians introduced a suite of plants as a crucial ecological aspect of their colonization of Tonga (e.g., Whistler 1991; Fall 2005, 2010; Prebble 2008). Subsequent European introductions include all species that arrived in Tonga following European contact (whether the plants originated in Europe, Africa, Asia, or the Americas; after Smith 1979–1991; Whistler 1995).

The seed dispersal mechanisms for each species were derived from more than sixty published sources, beginning with the seminal works of Ridley (1930) and van der Pijl (1982), as well as Carlquist's (1967, 1974) studies of Pacific island dispersal. We identify mechanisms ranging from active, ballistic dispersal, whereby the diaspore or seed is ejected from a plant, to passive mechanisms, including both biotic and abiotic vectors. Abiotic mechanisms feature dispersal by water (hydrochory) or wind (anemochory), whereas biotic vectors include internal animal dispersal (e.g., by birds or bats) in which an animal can carry seeds by mouth or consume and pass (sometimes scarifying) viable seeds in a new location. Alternatively, seeds might be dispersed externally (epizoochory) when a seed or diaspore is carried on the outside of an animal to a new location (e.g.,

involving attachment with burrs). Rodents can disperse seeds but also act as seed predators (Osunkoya 1994; Abe 2007; Meyer and Butaud 2009; Grant-Hoffman and Barboza 2010). Biotic mechanisms also pertain to dispersal by humans, including the cultivation of plant species. Our identification of cultivated species utilizes Whistler's (1991) detailed discussion of planting and cultivation on the Tongan islands.

Statistical Analyses and Results

Species–Area Relationships and Richness

To assess the factors underlying differences in species richness on the islands of Tonga, we use linear regression analysis to consider the relationship between the number of plant species on an island and (1) island area (a measure of habitat availability) and (2) maximum island elevation (a measure of environmental variability). The Kolmogorov–Smirnov normality test shows that the data for number of plant species and maximum elevation do not deviate significantly from a normal distribution. The data for island areas deviate significantly from a normal distribution, however, and are normalized as square roots. Endemic and indigenous species make up the majority of plant species on ten of the eleven Tongan islands investigated (Table 2). Tongatapu is the exception with the highest number of Polynesian and European introductions, which jointly represent approximately 59 percent of plant species. For the archipelago of Tonga, linear regression analysis shows that island area is indeed an effective predictor of species richness (Pearson's $r = 0.821$, $p < 0.002$), with larger islands supporting demonstrably greater numbers of species (Figure 2A; Table 3). When species richness is considered according to plant origins, an increase in endemic and indigenous species with greater island area could be deemed statistically insignificant ($p = 0.06$; Figure 2B). Significant increases in Polynesian introductions ($p = 0.008$) and European introductions ($p = 0.009$) with larger island area, however, accord clearly with the species–area relationship (Figures 2C and 2D). The numbers of plant species using each dispersal mechanism also increase with island size, especially those utilizing birds, bats, rodents, ants, and human cultivation (Table 4), as a collateral effect of the species–area relationship in which greater numbers of plant species entail correspondingly greater numbers of dispersal mechanisms, thus providing two interrelated expressions of this relationship.
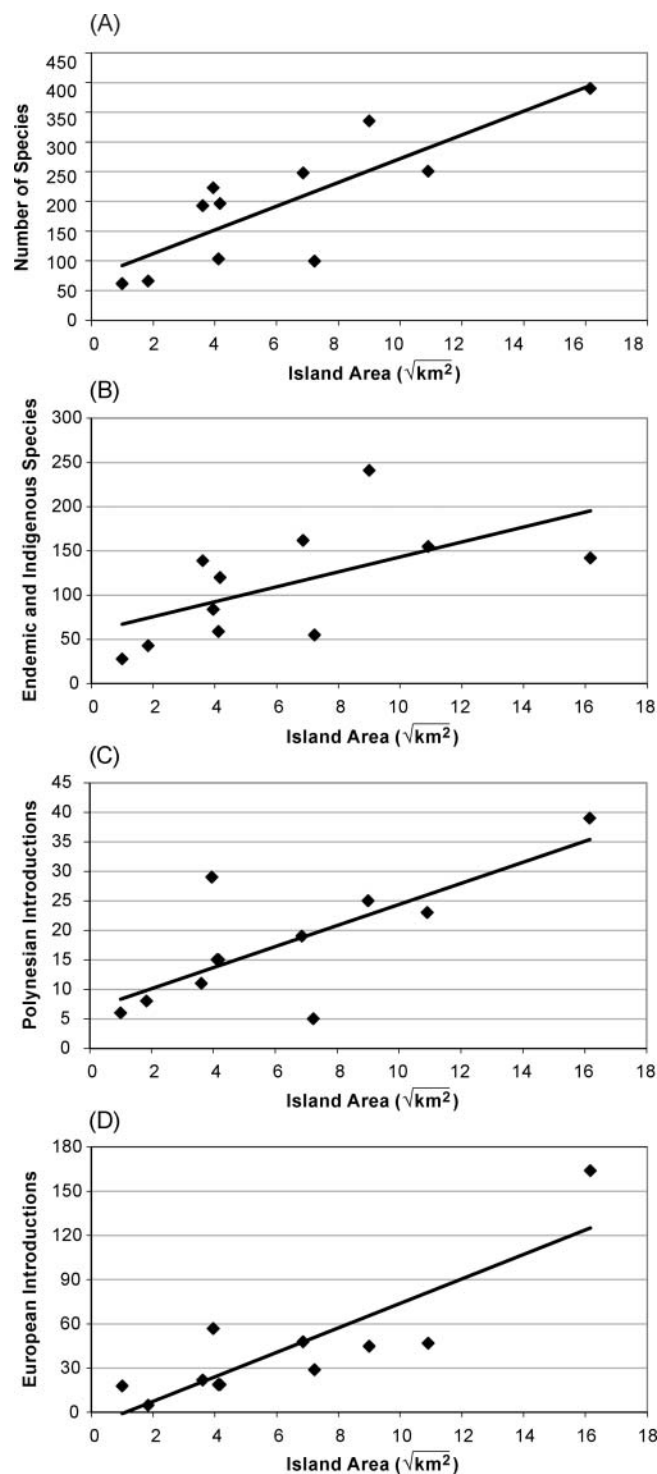
Figure 2. Species–area relationships by plant origins (data for island area normalized by using the area square root). (A) Regression of island area on the total number of species for all origin types. (B) Regression of island area on number of endemic and indigenous species. (C) Regression of island area on number of Polynesian introductions. (D) Regression of island area on number of European introductions. See Table 3 for associated statistics.

Table 3. Regression statistics for species–area relationships (SARs), species per island by maximum elevation (SMEs), and number of species by distance from Tonga to its nearest island neighbors, Samoa and Fiji

	Pearson's r	r^2	p
Species–area relationships			
SAR all species	0.821	0.674	**0.00197**
SAR indigenous/endemic	0.582	0.339	0.060
SAR Polynesian introductions	0.750	0.563	**0.008**
SAR European introductions	0.851	0.724	**0.0009**
Species by maximum elevation			
SME all origin types	0.003	0.000009	0.993
SME indigenous/endemic	0.746	0.557	**0.008**
SME Polynesian introductions	−0.516	0.266	0.104
SME European introductions	−0.646	0.417	**0.032**
Species by distance from nearest island groups			
Distance from Lau Group, Fiji	−0.326	0.106	0.330
Distance from Viti Levu, Fiji	−0.230	0.053	0.500
Distance from Samoa	0.440	0.194	0.180

Note: Significant regression equations shown in bold; i.e., $p < 0.05$.

In contrast to the results for island area, the relationship between island species counts and maximum elevation produces a nearly flat regression line and a correlation coefficient approaching zero (Figure 3A; Table 3), which seemingly suggests that plant species richness is effectively unrelated to elevational differences between islands. When expressed as relative frequencies, however, plant species data correlate with maximum island elevation differently according to origin type, revealing the importance of distinguishing the historical constituents of Tongan vegetation. The relative frequency of endemic and indigenous species grows significantly with increased maximum elevation ($p = 0.008$), whereas the percentage of European introductions drops significantly ($p = 0.032$) and the proportion of Polynesian species declines insignificantly ($p = 0.104$; Figures 3B–D; Table 3).

Species–Isolation Relationships and Richness

We expected the islands of Samoa and Fiji might be sources for Tongan plants, based on their relatively larger areas, their more diverse floras and faunas, and their greater proximity to mainland Asia, where we find

Table 4. Number and percentage (%) of plant species on the main Tongan islands according to dispersal mechanisms (species might have multiple dispersal mechanisms, thus percentages may exceed 100%)

	n	Wa	Wi	Bi	Bat	Epi	Cult	Ro	Ant	Bal
Limestone islands										
Tongatapu	373	190(51)	91(24)	249(67)	91(24)	88(24)	123(33)	28(8)	39(10)	22(6)
Vava'u	246	111(45)	52(21)	179(73)	87(35)	40(16)	58(24)	23(9)	14(6)	8(3)
'Eua	328	133(41)	102(31)	218(66)	100(30)	72(22)	43(13)	25(8)	24(7)	8(2)
E. Ha'apai	100	57(57)	14(14)	80(80)	41(41)	17(17)	36(36)	7(7)	9(9)	1(1)
'Euaiki	59	29(49)	18(31)	39(66)	17(29)	14(24)	11(19)	5(8)	7(12)	4(7)
Volcanic islands										
Niuafo'ou	99	43(43)	24(24)	67(68)	29(29)	21(21)	23(23)	5(5)	9(9)	4(4)
Tofua	234	101(43)	93(40)	130(56)	52(22)	70(30)	27(12)	12(5)	23(10)	10(4)
Late	188	84(45)	78(41)	109(58)	45(24)	44(23)	24(13)	12(6)	17(9)	2(1)
Niuatoputapu	219	120(55)	53(24)	159(73)	65(30)	45(21)	75(34)	17(8)	24(11)	9(4)
Kao	183	78(43)	78(43)	101(55)	38(21)	53(29)	14(8)	6(3)	12(7)	6(3)
Tafahi	63	24(38)	18(29)	46(73)	20(32)	15(24)	13(21)	3(5)	2(3)	1(2)

Note: Chi-square test of dispersal mechanism (water, wind, birds, bats, epi, cult) versus island (without Tafahi and 'Euaiki): $\chi^2 = 187.74$, minimum expected value: 20.77, $df = 40$, $p = 5.3 \times 10^{-21}$. Wa = Water; Wi = Wind; Bi = Birds; Bat = Bats; Epi = Epizoochory; Cult = Cultivated; Ro = Rodents; Ant = Ants; Bal = Ballistic.
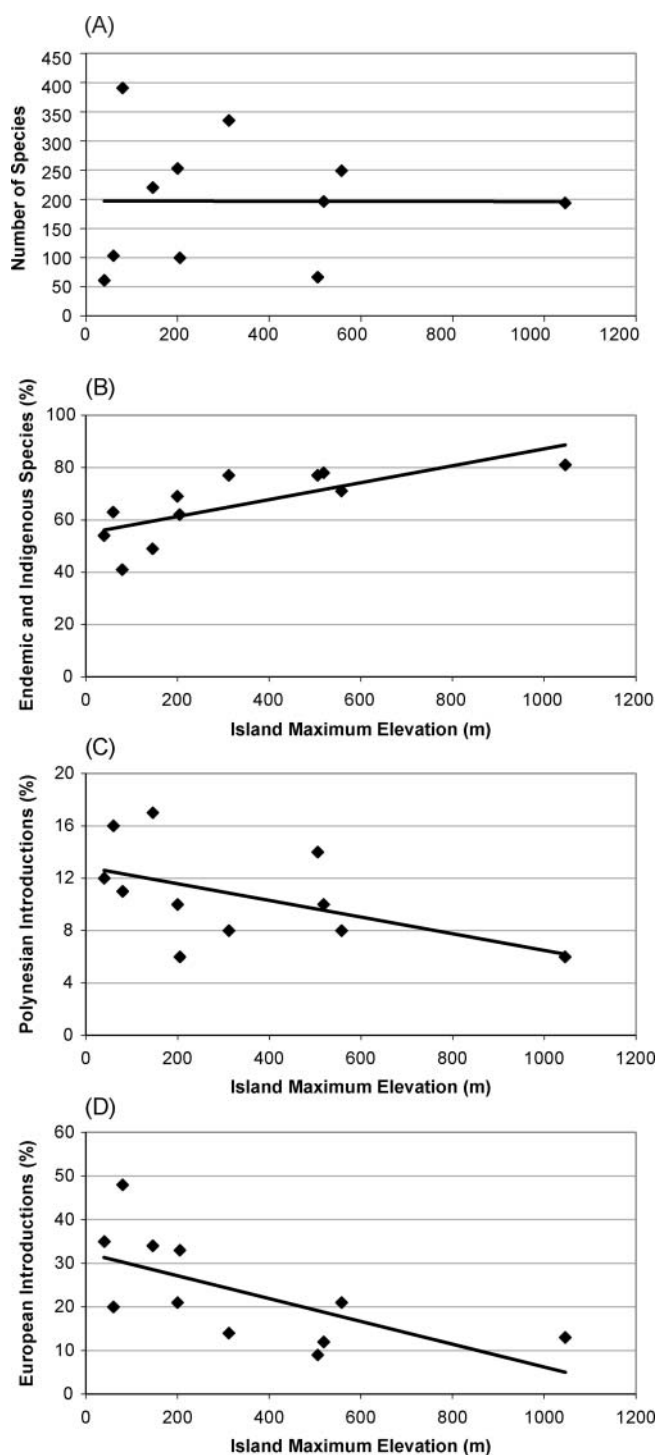
Figure 3. Number of plant species on the major islands of Tonga according to maximum island elevation. (A) Regression of maximum island elevation on the total number of species for all origin types. (B) Regression of maximum elevation on percentage of endemic and indigenous species. (C) Regression of maximum elevation on percentage of Polynesian introductions. (D) Regression of maximum elevation on percentage of European introductions. See Table 3 for associated statistics.

species with the greatest affinities to those on western Pacific islands. It is possible, however, that Tonga might have served as a source area for these archipelagoes. In this article we considered species richness for the islands of Tonga relative to each island's distance from the archipelagos of Samoa to the north and Fiji to the west. The Kolmogorov–Smirnov normality test shows that the data for island distances from Tonga to Samoa and Fiji do not deviate significantly from a normal distribution. Species richness for the islands of Tonga shows virtually no relationship to island distances from Samoa (measured from Savaii; $p = 0.18$) or Fiji (measured from the largest island of Viti Levu [$p = 0.5$], nor from the closest islands of the Lau Group [$p = 0.33$]). Linear regression shows that species counts for the islands of Tonga are consistently unrelated to distance from these neighboring archipelagos (Table 3).

We also investigated the relationship among Tonga, Fiji, and Samoa in terms of their geologies. The greatest floral similarities between Samoa and Tonga are found on the volcanic islands of each nation, suggesting the importance of geological substrate in determining island plant communities. The flora on Tonga's limestone islands is more similar to, although less species rich than, the vegetation of Fiji (Smith 1979–1991; Mueller-Dombois and Fosberg 1998; Franklin, Keppel, and Whistler 2008).

Plant Dispersal: Geology, Colonization, and Vegetation Types

Island geology emerges again as a major distinguishing factor in plant dispersal. The major biotic mechanisms of dispersal by birds, rodents, epizoochory, and humans are more common on limestone islands ($\chi^2 = 27.25$, $df = 6$, minimum expected value $= 8.13$, $p = 0.00013$), whereas the relative frequency of bat dispersal is comparable on both island types (Figure 4). Abiotic vectors involve greater dispersal by water on limestone islands in contrast to greater wind dispersal in volcanic settings. A comparison of the frequencies of seven dispersal mechanisms identifies the key difference as volcanic versus limestone geology. This result is based on twenty-one pairwise chi-square tests of bird, bat, water, wind, cultivated, epizoochorous, and rodent dispersal that produced six significant distinctions (i.e., $p < 0.05$), each of which compared wind with another dispersal vector. Accordingly, we infer a link between geologic substrate (e.g., volcanic) and favored dispersal vector (e.g., wind dispersal).
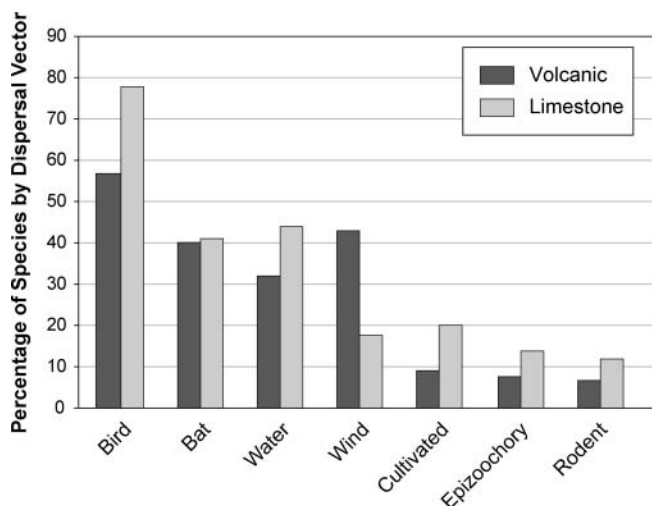
Figure 4. Percentages of lowland rain forest species by dispersal mechanism (birds, bats, water, wind, cultivated, epizoochory, and rodents) on volcanic and limestone islands in Tonga (chi-square based on species counts: $\chi^2 = 27.25$, $df = 6$, minimum expected value = 8.13, $p = 0.00013$).

Floral composition on the islands of Tonga reflects a blend of spatial, elevation, and geological influences in which the five islands with the greatest relative frequency of endemic and indigenous species, and more common wind dispersal, coincide with the five highest elevation islands, four of which are volcanic islands (Figure 5). In a complementary pattern, the six lower elevation, generally limestone, islands have higher percentages of European introductions and vegetation utilizing greater nonwind dispersal. The relative frequencies of plant species utilizing each dispersal type (Table 4) vary further according to topography and human intervention. The islands of Tongatapu, Ha'apai, and Niuatoputapu (with populations of

about 72,000, 7,500, and 1,000 respectively; see Table 1), with their low topographic relief, have the highest relative frequencies of cultivated plant species. Although the percentages of rodent-dispersed species vary minimally among islands, the greatest numbers of these species are found on the heavily inhabited islands of Tongatapu, Vava'u (about 15,000 people), and 'Eua (5,000+ people).

Dispersal mechanisms also assume differing importance according to the vegetation types found on the islands of Tonga (Table 5). Among the major abiotic vectors, the relative frequency of water-dispersed species generally increases, as expected, with the proximity of vegetation types to water. Dispersal by water is most substantial among littoral scrub and littoral forest and in mangroves, swamps, and wetlands. Wind dispersal is most common in relatively open volcanic and secondary rain forest vegetation, which features weedy, early colonizing species adapted to nonshady environments. In contrast, the percentages of bird- and bat-dispersed species are low in these open settings but highest in the denser vegetation of *Casuarina* forest and upland rain forest.

In conjunction with dispersal mechanisms, the vegetation types of the Tongan islands vary systematically according to plant origins, with a clear predominance of indigenous species in the upland rain forest, littoral scrub, and *Casuarina* forest (Figure 6). Lowland rain forest, volcanic vegetation, littoral forest, and mangroves, swamps, and wetlands feature more varied percentages of indigenous taxa, European introductions, and Polynesian introductions, in descending order. Secondary rain forest provides the lone vegetation type with a majority of introduced plants, especially European introductions. The effects of human disturbance on the
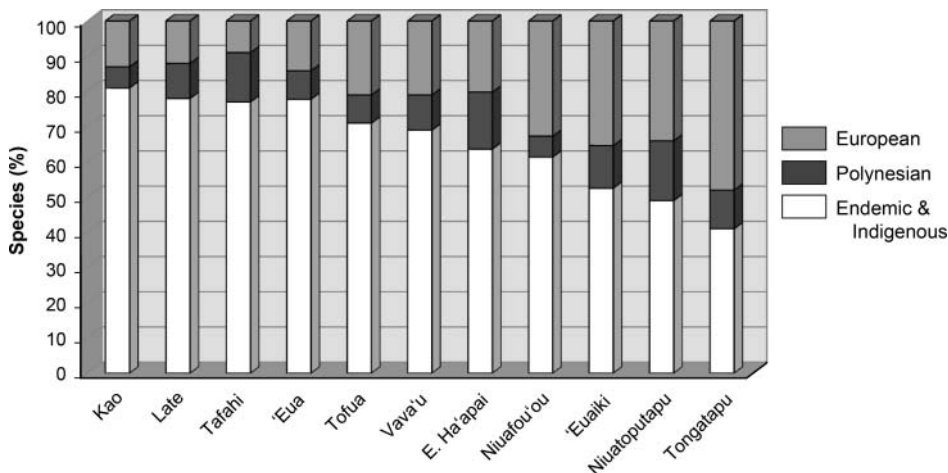

Figure 5. Species percentages of plant origin types on the major islands of Tonga (chi-square based on species counts: $\chi^2 = 200.42$, $df = 20$, minimum expected value: 5.35, $p = 9.31 \times 10^{-32}$).

Table 5. Number and percentage (%) of plant species dispersed by each dispersal mechanism according to vegetation type on the major islands of Tonga (species might have multiple dispersal mechanisms, thus percentages may exceed 100%). Vegetation types are listed according to generally increased distance from coastlines

	n	Wa	Wi	Bi	Bat	Epi	Cult	Ro	Ant	Bal
Mangrove and coastal swamps	50	33(66)	12(24)	35(70)	12(24)	12(24)	10(20)	5(10)	9(18)	2(4)
Littoral strand and scrub	65	58(89)	16(25)	48(74)	11(17)	20(31)	6(9)	3(5)	7(11)	2(3)
Littoral forest	100	56(56)	23(23)	75(75)	36(36)	17(17)	21(21)	13(13)	9(9)	1(1)
Casuarina forest	15	5(33)	2(13)	14(93)	7(47)	1(7)	2(13)	0(0)	3(20)	0(0)
Lowland rain forest	251	104(41)	63(25)	179(71)	95(37)	32(13)	43(17)	27(11)	15(6)	5(2)
Secondary rain forest	211	87(41)	71(34)	135(64)	47(22)	63(30)	26(12)	16(8)	33(15)	19(9)
Upland rain forest	63	10(16)	16(25)	49(78)	29(43)	8(13)	6(10)	8(13)	3(5)	1(2)
Volcanic vegetation	45	20(44)	17(38)	27(60)	11(24)	12(27)	6(13)	1(2)	8(18)	1(2)

Note: Chi-square test of dispersal mechanism (water, wind, birds, bats, epi, cult) versus vegetation type (without *Casuarina* forest): $\chi^2 = 97.0$, minimum expected value = 6.62, $df = 30$, $p = 5.5 \times 10^{-9}$. n = number of plant species with dispersal data; Wa = Water; Wi = Wind; Bi = Birds; Bat = Bats; Epi = Epizoochory; Cult = Cultivated; Ro = Rodents; Ant = Ants; Bal = Ballistic.

dispersal patterns of Tongan vegetation are illustrated by a comparison of species origins and dispersal vectors found in lowland rain forest and secondary rain forest ($\chi^2 = 32.60$, minimum expected value = 45.54, $df = 4$, $p = 1.44 \times 10^{-6}$; Table 6). The lowland rain forest, with its clear predominance of endemic and indigenous species, exemplifies less disturbed, largely natural vegetation, while secondary rain forest has 58 percent introduced species and reflects vegetation that succeeds the lowland rain forest in the wake of human disturbance ($\chi^2 = 75.05$, minimum expected value = 15.73, $df = 2$, $p = 5.05 \times 10^{-17}$). Among the crucial distinctions in dispersal patterns between these vegetation types, lowland rain forest shows a greater than expected reliance on dispersal by birds (179 observed species vs. 164 expected species) and bats (93 observed vs. 73 expected) associated with native species, whereas secondary rain forest utilizes greater than expected dispersal by wind (71 vs. 64), epizoochory (63 vs. 46), and human (78 vs. 67) behavior often associated with more open vegetation or forest disturbance (see Table 6). Among other animal vectors with connotations of introduced ecological change, rodents impact seed dispersal most actively in rain forests and swamps (see Table 5).

Discussion

This study marshals the vegetation geography of Tonga to assess the broad suite of factors that mold island plant dynamics. The explanation of biotic diversity in Tonga emerges in a variety of characteristics related to island sizes (species–area relationships), isolation, geology, plant origin types, and LDD.
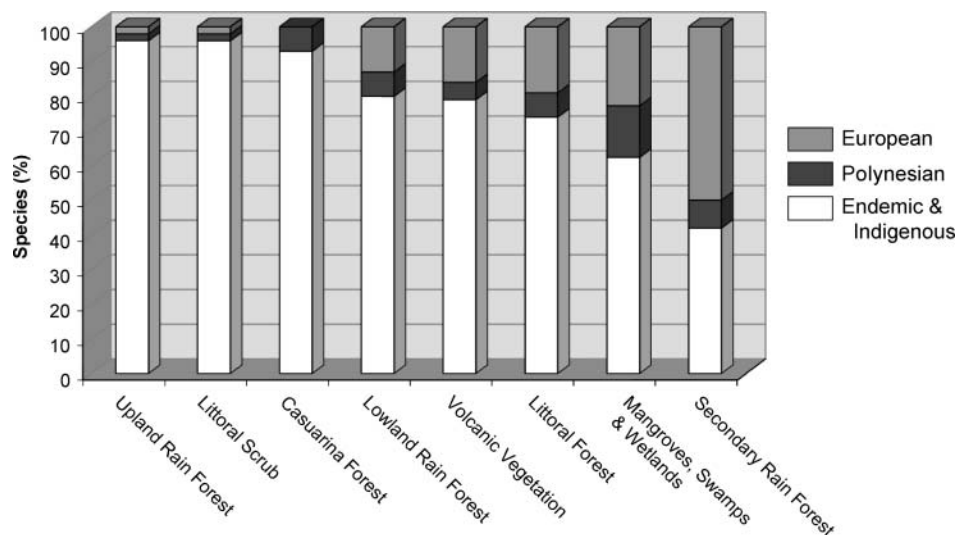

Figure 6. Species percentages of plant origin types (endemic + indigenous and Polynesian + European introductions) on the major islands of Tonga according to vegetation type excluding *Casuarina* forest (chi-square based on species counts: $\chi^2 = 130.45$, minimum expected value = 12.87, $df = 6$, $p = 1.03 \times 10^{-25}$).

Table 6. Observed (and expected) numbers of plant species in lowland rain forest compared to secondary lowland rain forest

	Lowland rain forest	Secondary rain forest
Wi	63 (69.8)	71 (64.2)
Bi	179 (163.5)	135 (150.5)
Bat	93 (72.9)	47 (67.1)
Epi	32 (49.5)	63 (45.5)
Hu	61 (72.4)	78 (66.6)
E + I	190 (148.3)	86 (127.7)
Poly	17 (18.3)	17 (15.7)
Eur	31 (71.5)	102 (61.5)

Note: Chi-square for dispersal mechanisms: $\chi^2 = 32.60$, minimum expected value $= 45.54$, $df = 4$, $p = 1.44 \times 10^{-6}$. Chi-square for species origins: $\chi^2 = 75.05$, minimum expected value $= 15.73$, $df = 2$, $p = 5.05 \times 10^{-17}$. Wi = Wind; Bi = Birds; Bat = Bats; Epi = Epizoochory; Hu = Human; E + I = Endemic and indigenous; Poly = Polynesian; Eur = European.

Species–Area Relationships and Richness

In the archipelago of Tonga, species richness reflects a variety of influences based on species–area relationships. In keeping with a fundamental component of the theory of island biogeography, island area affects richness profoundly. More subtle variations between plant origin types as they relate to the species–area relationship and habitat diversity (based on island elevation) suggest the importance of interpretation of human-induced LDD in the development of island floras. In this case, Polynesian and European introductions, but not endemic and indigenous species, are significantly more abundant on larger islands. In contrast, although overall species richness and island elevation appear to be unrelated, native species are more abundant on higher elevation islands, and introduced species diminish with increased elevation. Thus, species–area relationships vary considerably, and might even diverge, when plant origins are taken into account.

Patterns of plant dispersal reflect the pronounced potential for vegetation change on islands with low topography, which implies greater suitability for human settlement, plant management, and the introduction of new plant and animal species. This avenue of change potentially involves the introduction of new vegetation, including cultigens and dispersal vectors such as introduced birds and rodents, and epizoochory, with associated impacts on native dispersers (e.g., bats). Interestingly, the islands with the highest percentages of endemic and indigenous species (Kao, Late, Tafahi, 'Eua, Tofua; Figure 5) tend to share higher elevations and volcanic geology (with the exception

of 'Eua), whereas the islands with greater percentages of introduced flora are lower, more heavily inhabited, and limestone (Tongatapu, Niuatoputapu, 'Euaiki, Niuafou'ou, E. Ha'apai, Vava'u).

Species–Isolation Relationships and Richness

As noted earlier, the greater diversity and richness of the floras of Samoa and Fiji make them logical candidates to have been source areas for the vegetation in Tonga. The islands of Tonga reveal no patterns of species richness related to island proximity to Samoa or Fiji, however. Instead, and in accordance with the importance of island geology found in other aspects of this study, floral similarities are clearest between islands in these archipelagoes that share common geologies. Thus, somewhat unexpectedly in light of the tenets of the Theory of Island Biogeography, the species–isolation relationships between Tonga and its nearest Pacific island neighbors appear unrelated to interisland distance. This result, however, is in keeping with recent studies that show that rare long-distance introductions (in which we include the influences of human colonization) might be more important than the cumulative effects of more frequent events involving generalized dispersal (e.g., Kot, Lewis, and van den Driessche 1996; Clark et al. 1999; Baudouin and Lebrun 2009).

The importance of broadening biogeographic research on plant dispersal, especially LDD, to encompass polychory, dispersal by multiple dispersal mechanisms, has been stressed by Berg (1983) and more recently by Nathan et al. (2008). This shift in perspective is of particular relevance to island floras, which are dominated by species with multiple dispersal mechanisms and LDD. Most island plant species utilize more than one dispersal vector, first to cross long oceanic distances and subsequently to occupy the variety of habitats found on Pacific islands (e.g., Carlquist 1974). The prevalence of some dispersal vectors strongly reflects the geographic situation of vegetation communities, as exemplified most notably by water dispersal, which particularly characterizes littoral and coastal scrub species, swamps, and coastal and littoral forest.

Plant Dispersal: Geology, Colonization, and Vegetation Types

Dispersal adaptations often are associated with the life history of species and reflect their geological setting. Generally, vegetation types lie along a continuum from early to late succession that is characterized by species

that also vary along this continuum, as do the dispersal spectra for each vegetation type. Among the dispersal spectra in Tonga, we found that wind-dispersed species often are early successional and associated with disturbed areas, as documented elsewhere (Whittaker, Bush, and Richards 1989; Brown 1992; Ohtsuka 1999; Drezner, Fall, and Stromberg 2001), as well as being early colonists on volcanic islands (Gentry 1982; Whittaker et al. 1992; Whittaker and Jones 1994). The greatest proportion of Tonga's wind-dispersed flora is found among relatively open, early successional communities on volcanic islands and in disturbed habitats, particularly in the secondary lowland rain forests. Interestingly, the wind-dispersed floras of Tonga's limestone and volcanic islands are largely disparate, in keeping with the clear distinction in the frequencies of dispersal vectors found on volcanic versus limestone islands. About three quarters of the wind-dispersed species on limestone islands are absent from the volcanic islands, and about 70 percent of the wind-dispersed species on volcanic islands are not found on limestone islands.

The combined influences of island area, maximum elevation, and geology lead to high elevation, commonly volcanic islands with frequent native species. Birds and bats are particularly important agents of native plant dispersal; for example, in the Tongan upland and lowland forests, which are characterized by relatively high numbers of endemic and indigenous plants. Further, bird- and bat-dispersed species are important components of the community, providing food sources for native bird and bat species. Humans have impacted the flora of the Tongan archipelago over the last 3,000 years and continue to impact it today. Human populations alter the rain forests not only by deforestation and landscape change but also through dramatic changes to dispersal spectra. This effect is manifested in Tonga by lower elevation, commonly limestone islands with floras that include more abundant European introductions, which often are early successional and might be weedy or invasive (Whittaker, Bush, and Richards 1989; Bush and Whittaker 1991; Brown 1992; Drezner, Fall, and Stromberg 2001). Dispersal spectra assume further differences in importance in Tonga according to vegetation types and plant origins. Biotic dispersal, especially by birds and bats, is particularly important in denser, less disturbed native vegetation. Abiotic dispersal (e.g., wind, water) is more prominent in more open forest, littoral, or wetland vegetation in which disturbance has led to more abundant introduced species. Thus, humans have acted as agents of LDD, not only through the introduction of new plant species, but also through the accompanying wholesale reconfiguration of dispersal guilds and, thereby, the ecosystems that they perpetuate.

Conclusions

This discussion of plant species richness, species isolation, habitat diversity, and plant dispersal in Tonga leads to several inferences related to our original hypotheses.

1. The vegetation patterns of Tonga conform to the principles of the species–area relationship in a variety of aspects according to island area, elevation, and species origin. Island size, rather than elevation or habitat diversity, is a better predictor of species richness. Although the species–area relationship constitutes one of ecology's few laws (Whittaker and Triantis 2012), relatively few studies distinguish the differences in these relationships between native and introduced plant species. This article shows that the value of island size for predicting species richness, although true for all species combined, is also valid for nonnative introduced species. Further examination of species–area relationships by origin type shows that the relative frequencies of native species and of modern introductions are significantly related to elevation, whereas the numbers of Polynesian introductions do not conform to the predicted pattern, likely due to the more concentrated human settlement at lower elevations.

2. Vegetation diversity among the islands of Tonga, and between this archipelago and neighboring island groups, will demonstrate interisland biogeographic relationships based on island isolation and geology. The islands of Tonga do not reveal the species affinities predicted by species–isolation relationships with Samoa or Fiji, nor does its vegetation show the high rates of endemism predicted for islands that are isolated from source areas. Instead, Tonga's island floras appear to have derived less from (nor contributed to) neighboring archipelagoes than from "jump dispersal" (Pielou 1979), which included human colonization as a major vector of LDD. Ancient Polynesian introductions also might involve jump dispersal as distinct from island hopping. As a case in point, DNA studies demonstrate that coconut trees in the Americas derived from the Philippines

rather than from Pacific island source areas (Baudouin and Lebrun 2009), supporting an inference of historic or prehistoric human LDD. Ecological communities are influenced profoundly by variations in substrates (in the case of Tonga, limestone or volcanic), which serve as proxies for island age. High volcanic islands have the highest frequencies of native species, whereas the lower, more settled, limestone islands have greater representations of nonnatives and generally higher numbers of species in total. The typically more weedy and early successional wind-dispersed species are most common on volcanic slopes and in disturbed forest.

3. The incorporation of plant dispersal data with vegetation type, geology, and plant origins will reveal that Tongan biogeographic change is heavily predicated on the effects of plant and animal introductions and human behavior on the plant dispersal spectra of Tonga. This analysis of biogeographic dynamics incorporates the variety of ways in which island vegetation might be altered or disrupted. Incorporation of vegetation type, species origins, and LDD provides a means of exploring integrated ecological change, especially as the introduction of new species leads to shifting configurations of plant dispersal. Tonga's dispersal spectra reflect the compounded influences of island geology, topography, and human intervention, and they make Tonga's vegetation types differentially susceptible to biogeographic change. Differences in plant origins play a fundamental role in variable vegetation changes and their dispersal vectors on the islands of Tonga. For example, native vegetation, especially when minimally disturbed, remains particularly reliant on bird and bat dispersal. More open vegetation types in particular tend to reflect dispersal shifts resulting from disturbance, especially when culturally induced. The vegetation in Tonga most vulnerable to this form of change includes lowland and littoral rain forests and wetlands (mangroves and swamps). For example, Polynesian introductions are especially prevalent in vegetation types reflecting human disturbance, such as lower elevation rain forest and wetlands. In contrast to the greater bird and bat dispersal characteristic of native vegetation, the impacts of disturbance include increased frequencies of epizoochorous (adhesive) and human cultivated or dispersed species, often as modern introductions. Accordingly, European introductions are dramatically overrepresented in the disturbed rain forest and underrepresented in the lowland rain forest, whereas the opposite is true of native species. Thus, an integrated consideration of the distinct factors molding an island's biogeography, including its environmental variability, LDD, and ancient and modern species origins, contributes to a nuanced understanding of the biogeographic dynamics of Tonga and island ecosystems generally.

This article highlights the roles of LDD, multiple dispersal mechanisms, and ancient and modern human-introduced species and dispersal vectors, all of which need to be incorporated into future discussions of island biogeography.

Acknowledgments

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