Cyclones influence native plant diversity on 22 remote high islands of French Polynesia and Pitcairn (eastern Polynesia)

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Cyclones influence native plant diversity on 22 remote high islands of French Polynesia and Pitcairn (eastern Polynesia)

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I examined the relative influence of eight spatial characteristics on native plant diversity in 22 volcanic high islands of eastern Polynesia. The characteristics used as potential predictors in this study included island area, highest elevation, distance to the nearest continent, distance to the nearest archipelago, distance to the nearest similar island, index of isolation, distance to the largest and highest island of Tahiti, and distance to the "cyclonic alley." Among characteristics studied, native plant diversity (indigenous and endemic species) was primarily linked with the island area and highest elevation of the islands. Contemporary cyclones were an important predictor of indigenous plant diversity in the remote islands surveyed. In the study area, this result suggests that cyclones, moving from the west Pacific Ocean basin to the eastern Polynesian islands, have provided more indigenous species to the remote high islands located close to the cyclonic alley. Isolation did not appear as a significant predictor of native plant diversity in the high islands surveyed, possibly due to a stepping-stone-island effect and the proximity of the cyclonic alley. These findings suggest that isolation could be tempered by a cyclonic-transport-flow effect in the study area, thus reducing the effective distance of the remote islands from the mainland source pool for seed dispersal.

Keywords: abiotic factors; cyclone alley; eastern Polynesia; island biogeography; native plant diversity

Introduction

How species reach islands and which factors influence native plant diversity are of particular interest to biogeographers. The relationships between the spatial characteristics of islands and native species richness have been studied by many workers (e.g. Gilbert, 1980; Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007), following MacArthur and Wilson (1967). The contrast in topography and substrata of high islands vs. coral atolls, as well as the total rainfall and average temperatures, are some factors influencing species richness on islands (Mueller-Dombois, 2002; Stoddart, 1992). However, Kalmar and Currie (2006) underlined that the literature addressing factors that determine species richness on islands contains an important gap, possibly due to different scales of analysis (Whittaker, Willis, & Field, 2001).

In particular, the size, elevation, or isolation of high islands are important features to explain diversity and endemism (e.g. Ackerman, Trejo-Torres, & Crespo-Chuy, 2007; Diamond, 1975; McMaster, 2005; Paulay, 1994; Preston, 1962a, 1962b;

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Rosenzweig, 1995). For example, Hamilton, Rubinoff, Barth, and Bush (1963) and Johnson and Raven (1973) concluded that elevation is significant for plant diversity in the Galapagos Archipelago. On the islands of the northeast coast of Australia, Buckley (1985) showed the influence of both elevation and substrate type on plant diversity. Losos and Schluter (2000) demonstrated that the size of the island influences the speciation, whereas Rosindell and Phillimore (2011) showed that speciation is strongly influenced by isolation. On the other hand, some results on bird diversity at global scales showed that this was best predicted on islands by a combination of isolation and/or size with other simple contemporary abiotic factors (Kalmar & Currie, 2006). Felicísimo and Muñoz (2012), and Muñoz, Felicísimo, Cabezas, Burgaz, and Martinez (2004) showed that floristic similarities, at large geographic scale, were better correlated with contemporary trade wind connectivity than with geographic isolation in the Southern Hemisphere. These studies support the hypothesis that wind is an important long-distance dispersal vehicle for native plants in the South Pacific Ocean. In addition, ocean currents or tropical cyclones could also be important to predict native plant diversity on the remote Pacific islands (e.g. Daehler, 2006; Dahl, 1984).

The physical disturbances of forest ecosystems by tropical cyclones have been described by many authors (e.g. Basnet, Likens, Scatena, & Lugo, 1992; Pascarella, Aide, & Zimmerman, 2004; Simberloff, 1995; Vandermeer, de la Cerda, Boucher, Perfecto, & Ruiz, 2000; Walker, 1991) and specifically their impacts on lowland rain forests of tropical islands (Hastings, 1990; Kerr, 2000; Lugo, 2008). Damages reported ranged from moderate effects, i.e. broken branches, defoliation, and tree falls (e.g. Elmqvist, Rainey, Pierson, & Cox, 1994; Turton & Siegenthaler, 2004), to important effects with high tree mortality (Franklin, Drake, McConkey, Tonga, & Smith, 2004; Lugo, 2008; Zimmerman et al., 1994). Some tree species are more vulnerable to cyclonic winds (Burslem, Whitmore, & Brown, 2000; Curran et al., 2008; Elmqvist et al., 1994; Herbert, Fownes, & Vitousek, 1999) and this selective mortality influences structure and composition of the tropical rain forests in the long term (Keppel, Buckley, & Possingham, 2010). Indeed, lower canopies and higher tree densities on the windward coast of Madagascar (de Gouvenain & Silander, 2003) and in Southwest Pacific islands (Keppel et al., 2010) have been related to the high frequency of cyclones in these regions. In the long term, a high frequency of cyclones disturbance drives diversity not only in tree communities (de Gouvenain & Silander, 2003; Keppel et al., 2010), but also in non-arborescent understory communities where an increasing diversity of ferns and vines was observed in Puerto Rico (Royo, Scalley, Moya, & Scatena, 2011). These findings contrast with prior assumptions, e.g. by Brokaw and Walker (1991), who reported that cyclones do not have a long-lasting impact on forest structure and composition, and support the hypothesis that cyclone disturbance is an important factor controlling, at least partially, forest structure and plant diversity in tropical islands. In addition, some studies reported that high frequency of storm-induced disturbance may impact species richness in the Bahamian islands (Morrison, 2002), while Keppel et al. (2010) observed no significant effect of cyclone frequency on species diversity in the Southwest Pacific islands. However, no quantitative information is available about the influence of these long-distance dispersal vehicles on native species richness in eastern Polynesia.

In this study, several predictors were tested to explain the native plant diversity in the remote islands of eastern Polynesia. Among these predictors, I closely examined if the number of native plants on 22 remote high volcanic islands was related to the distance to the "cyclonic alley" (Figure 1). Here, the pathway of disturbance is explicitly considered as a spatial factor. I hypothesized that native species richness on the remote

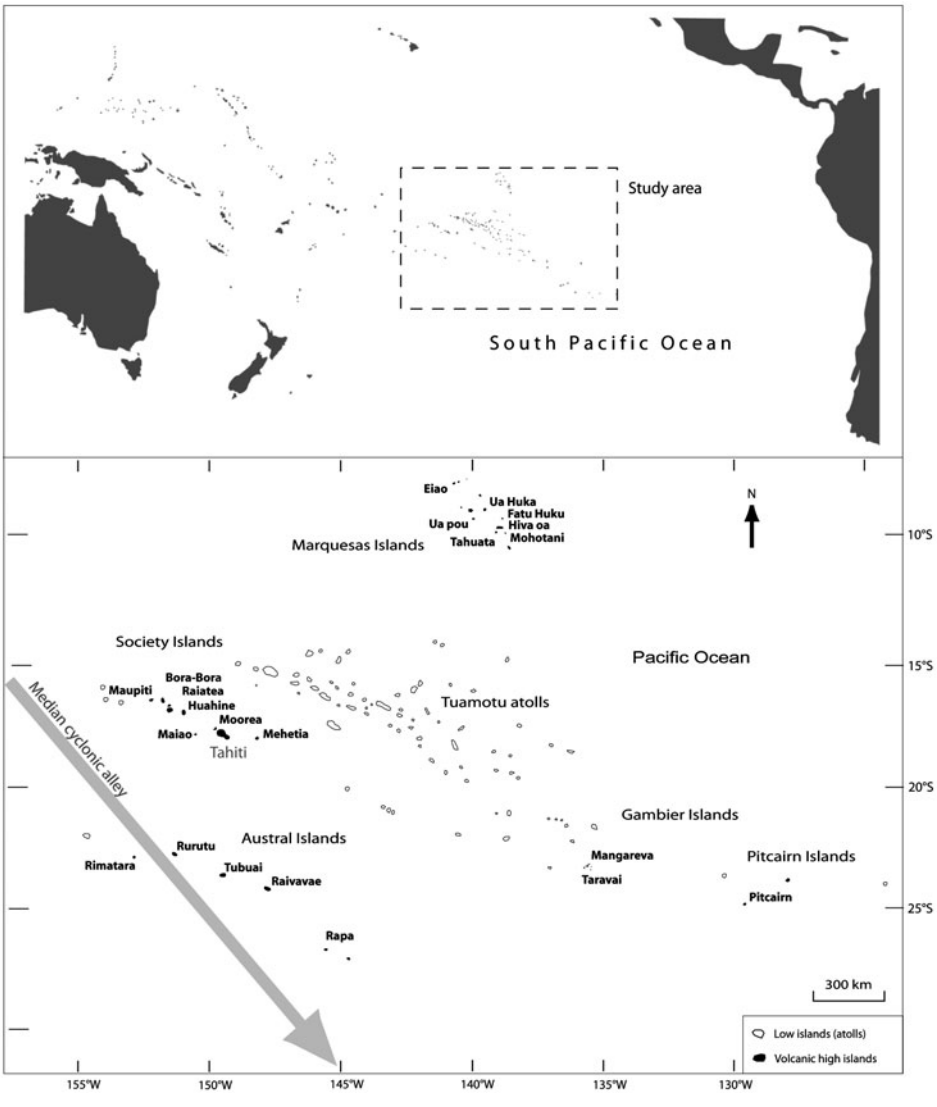

Figure 1. Location of the volcanic high islands in French Polynesia and the Pitcairn group (eastern Polynesia).
Notes: The 22 volcanic high islands surveyed in this paper appear in bold. The mapped "cyclonic alley" corresponds to the median cyclonic pathway followed by cyclones and tropical storms in the oceanic Economic Exclusive Zone (EEZ) of French Polynesia (for details see Etienne, 2012; Larrue & Chiron, 2010).

high islands of eastern Polynesia could be inversely related to the distance of these islands from the tropical cyclone pathway.

Materials and methods

Study area and islands surveyed

The study area corresponds to the geographic center of eastern Polynesia, which is formed by diverse volcanic and coral islands with marked geographic isolation in the

vast South Pacific Ocean. Eastern Polynesia is a large phytogeographical sub-region of Polynesia (Mueller-Dombois & Fosberg, 1998). It includes the five archipelagos of French Polynesia (i.e. the Society Islands, the Austral Islands, the Gambier Islands, the Marquesas Islands, and the Tuamotu atolls), and the archipelagos of the Cook Islands, the Pitcairn Islands, and Easter Island (Mueller-Dombois & Fosberg, 1998). With an island area of 1042 km² and a summit at 2242 m asl, the volcanic island of Tahiti (Society Islands, French Polynesia) is both the biggest and highest island of eastern Polynesia.

The islands surveyed consist of 22 volcanic high islands scattered in the tropical Pacific Ocean between 7°59′40.8″S – 25°04′08.5″S and 128°19′11.02″W – 154°38′33.06″W. Twenty-one of the islands are found in the volcanic archipelagos of French Polynesia, and one is located in the Pitcairn group (Figure 1). The islands surveyed represent a total terrestrial area of 1306 km², with a mean size of 59.3 km² and a mean elevation of 603 m. These small oceanic islands emerged from the basaltic bottom of the ocean (called a "hotspot") and were consequently never connected to a mainland (Allison & Eldredge, 1999; Mueller-Dombois, 2002; Nunn, 1994). These islands are among the most isolated in the world and native species in eastern Polynesia mark the "easternmost limit of the range of a very large number of genera in Malaysia and Pacific Ocean islands" (Meyer, 2004, p. 363). These islands are hit by cyclones, but the average frequency of disturbance (cyclone by year) is very low in the study area, i.e. 0.12 per year between 1970 and 2009 (Larrue & Chiron, 2010).

Methods

Characteristics of islands analyzed in this study

According to their potential influence on the native diversity, the following characteristics of the islands were selected: distance of each island to the nearest continent, distance to the nearest archipelago, distance to the nearest similar island, distance to Tahiti, distance to the cyclonic alley, isolation, island area, and highest elevation. Each measurement of distance was performed with a Geographic Information System (GIS Mapinfo® Professional version 10, WGS 1984 projection). With regard to the characteristic distance to Tahiti, note that this both largest and highest island was chosen in relation to the potential "stepping-stone effect" reported by workers in some other archipelagos (MacArthur & Wilson, 1967; McMaster, 2005).

AQ1 The data for island area and highest elevation were obtained from the Atlas of French Polynesia (Dupon, 1993) and United Nations Environment Programme (UNEP) island database (http://islands.unep.ch). The index of isolation was calculated as defined by the UNEP index of isolation (Dahl, 1998) as:

$$I_i = \left(\sqrt{d_i} + \sqrt{d_a} + \sqrt{d_c}\right),$$

where d_i is the distance to the nearest equivalent or larger island, d_a the distance to the nearest archipelago, and d_c, the distance to the nearest continent (i.e. North America, South America, Australia, or New Guinea).

Selection of 22 volcanic high islands

The selection of the islands surveyed was made in two steps. First, the volcanic high islands (> 0.5 km²) of French Polynesia and Pitcairn group were listed based on the

Atlas of French Polynesia (Dupon, 1993) and the UNEP island database (http://islands.unep.ch). Thirty-three volcanic high islands were found in the study area (Figure 1). Second, it is well known that island area and highest elevation are both important predictors for species richness on islands (e.g. Ackerman et al., 2007; McMaster, 2005; Triantis, Mylonas, Lika, & Vardinoyannis, 2003; Whittaker & Fernández-Palacios, 2007; Wright, 1983), and island isolation is an explanatory factor for diversity (e.g. Dahl, 1984; Meyer, 2004). Therefore, I used Multiple Correspondence Analysis (MCA, XLStat® [version 2007.6] software) with criteria of "island area," "highest elevation," and "isolation" to test the similarity of the volcanic high islands found in the study area (Figure 2). Then, an equal number of islands with a similar value of "island area," "highest elevation," and "isolation" were selected in pairs. These islands are similar in most respects, but present a maximum range of distance "to the cyclonic alley" (Table 1). Thus, 22 volcanic high islands scattered in the study area were selected and Spearman's correlation coefficients were used to confirm the independence of "island area" and "highest elevation" against the other characteristics in the islands selected (Figure 3).

Diversity of native plant species on the high islands

For each volcanic high island, I recorded both plant status and number of native plants listed in the online database Nadeau (Florence, Chevillotte, Ollier, & Meyer, 2007).

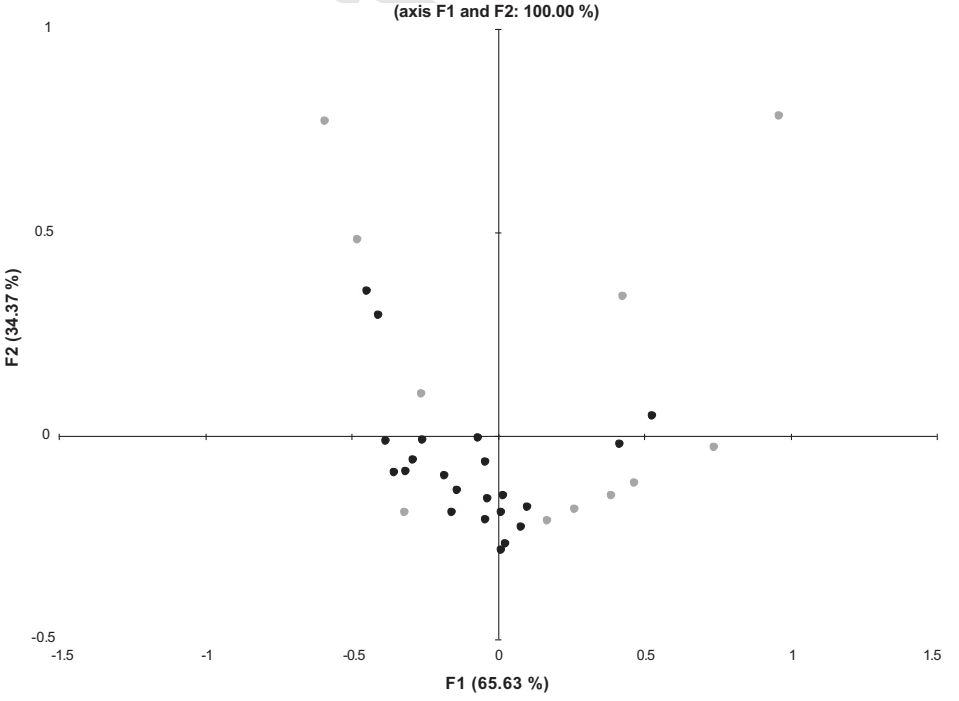

Figure 2. Multiple Correspondence Analysis (MCA) of the 33 volcanic high islands found in French Polynesia and the Pitcairn group with "island area," "highest elevation," and "isolation."
Notes: MCA shows an important range of these characteristics. Black circles correspond to the 22 high islands selected for this study.

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Table 1. Native plant diversity and characteristics of the 22 volcanic high islands surveyed in French Polynesia and Pitcairn (eastern Polynesia).

Pair of islands	Island area (km²)	Highest elevation (m)	Distance to the cyclonic alley (km)	Distance to Tahiti (km)	Distance to the nearest continent (km)	Distance to the similar island (km)	Distance to the nearest archipelago (km)	Index of isolation (UNEP)	Native plant diversity		Total native species richness
									Native but not endemic	Endemic species	
Fatu Huku (Marquesas)	1.3	360	3834	1430	4850	28	639	100.0	4	1	5
Mehetia (Society)	2.3	435	1278	180	6024	111	224	103.1	37	5	42
Pitcairn (Pitcairn)	4.2	347	4284	2134	5426	195	540	110.8	49	17	66
Taravai Gambier)	5.7	256	2891	1680	5739	5	213	93.6	17	3	20
Rimatara (Austral)	9	83	47	660	5373	148	528	108.4	73	8	81
Maiao (Society)	8	154	935	100	5789	100	350	104.7	25	0	25
Mangareva (Gambier)	13	441	2848	1680	6066	198	213	106.5	67	12	79
Maupiti (Society)	13.5	380	821	300	5700	50	461	104.0	56	8	64
Mohotani (Marquesas)	15	342	3734	1390	4941	35	532	100.2	24	11	35
Raiavavae (Austral)	20	437	585	740	5825	189	520	101.7	124	40	164
Bora Bora (Society)	29	727	878	250	5722	40	390	101.7	108	33	141

Tahuata (Marquesas)	61	1050	3691	1350	4811	7	532	95.0	74	62	136
Eiao (Marquesas)	43.8	576	3727	1430	4944	10	852	105	34	12	46
Rapa (Austral)	40	650	785	1040	6013	530	755	128.0	109	84	193
Huahine (Society)	74	669	942	170	5782	35	308	99.5	123	42	165
Tubuai (Austral)	45	422	377	660	5672	210	604	114.3	128	38	166
Ua Huka (Marquesas)	83	857	3784	1410	4751	49	852	106.8	83	51	134
Rurutu (Austral)	32	412	179	580	5524	210	555	111.1	128	25	153
Ua Pou (Marquesas)	111	1231	3655	1320	4800	50	770	104.1	82	54	136
Moorea (Society)	142	1207	1042	15	5862	15	219	95.2	172	94	266
Hiva Oa (Marquesas)	318	1190	3705	1380	4789	142	852	110.3	105	93	198
Raiatea (Society)	238	1017	863	198	5736	165	350	107.2	171	124	295

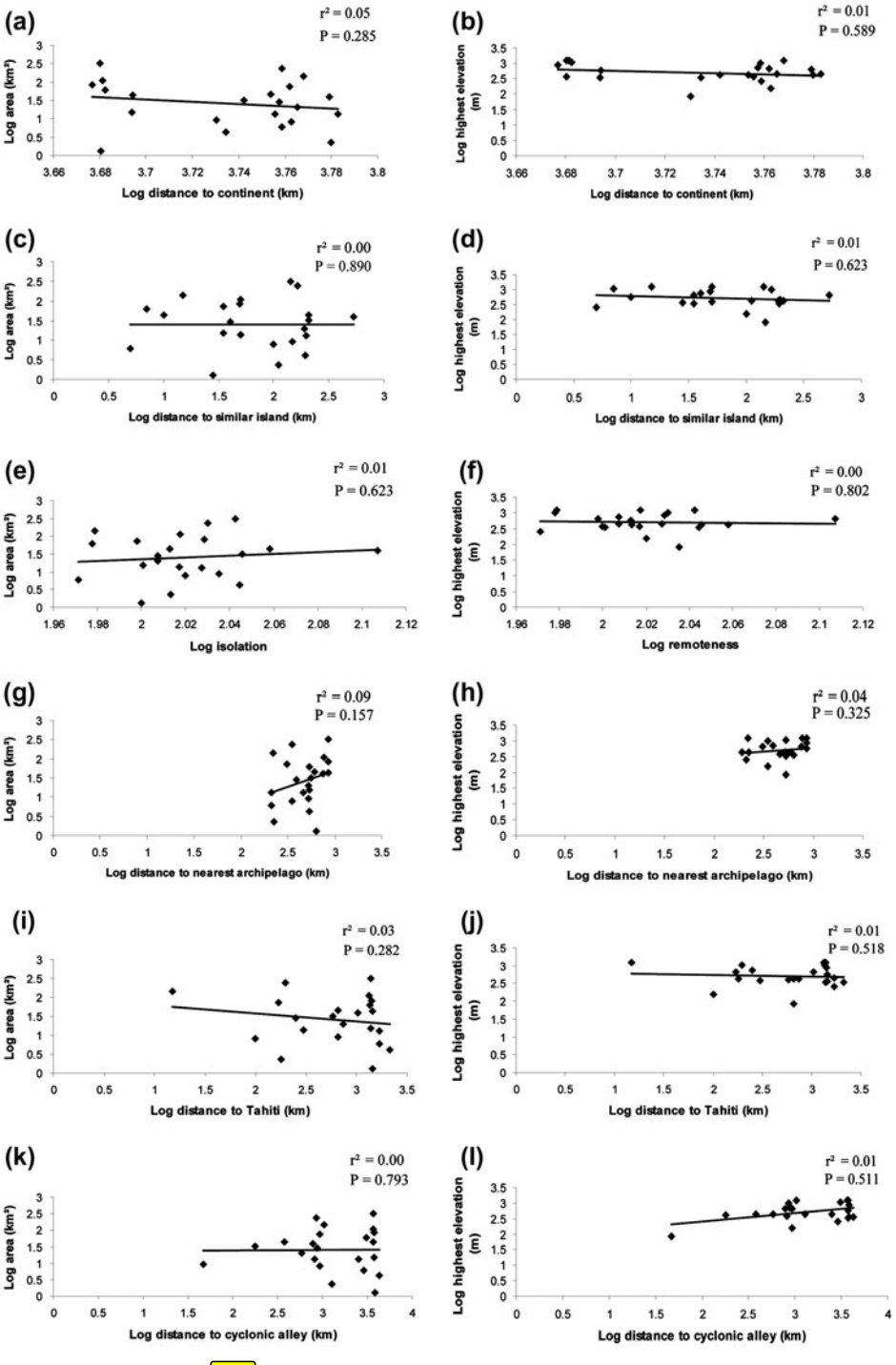

Figure 3. (a–l) Regressions of "island area" and "highest elevation" against the other independent variables for the 22 high islands surveyed (eastern Polynesia).

According to the database, the status of native species was listed as indigenous (i.e. native but not endemic) or endemic. Endemic species include four levels of endemism (Florence et al., 2007): (1) native species only found on an island and called "endemic insular," (2) species found in one archipelago and named "endemic archipelago," (3) species observed in the five archipelagos of French Polynesia and called "endemic French Polynesia," and (4) species that can be observed on the volcanic high islands of French Polynesia, the Pitcairn group, and Cook Islands, called the "endemic in eastern Polynesia."

Correlation between native plant diversity and characteristics of the 22 high islands

I tested the statistical correlations between each characteristic of the islands and native plant diversity (Spearman's correlation coefficients, Xlstat software). The statistical link between the native species richness and the distance to the cyclonic alley was closely observed.

Results

Native species richness on the 22 volcanic high islands

The indigenous species range from 4 to 172 species per island, and the total endemic species range between 0 and 124 species per island (Table 1). Indigenous and endemic status represent 68.6 and 31.4% of the native species found on the high islands surveyed, respectively (Figure 4). Figure 5 provides a detail of the native species richness found in the islands surveyed.

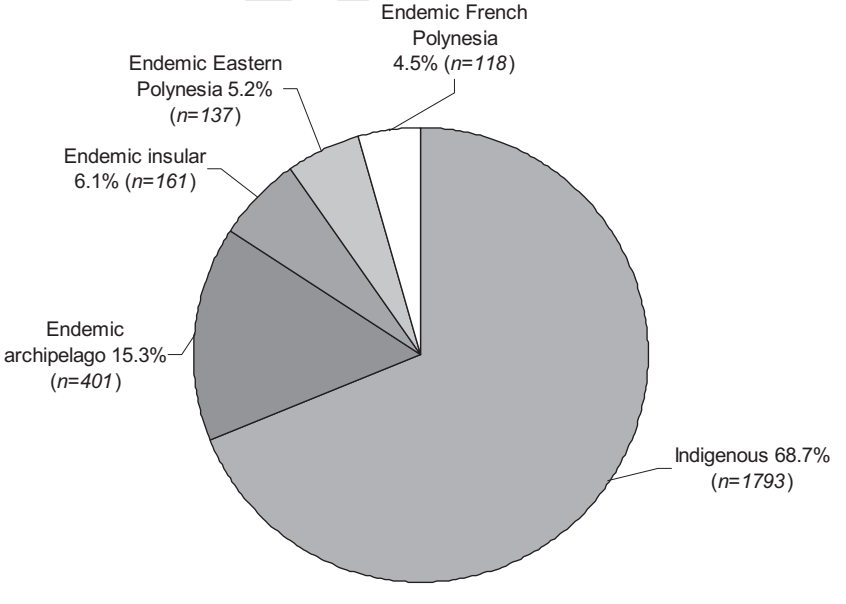

Figure 4. Distribution of native plants relative to status on the 22 high islands of French Polynesia and Pitcairn (eastern Polynesia).
Note: Note that *n* corresponds to the total citations of the status recorded on the 22 high islands.

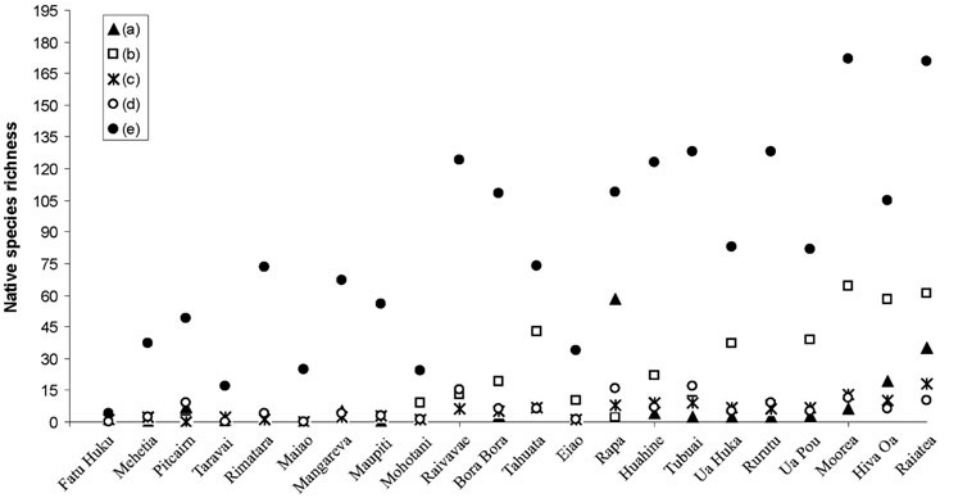

Figure 5. Native species richness in the 22 islands surveyed with: (a) "endemic insular," (b) "endemic archipelago," (c) "endemic French Polynesia," (d) "endemic in eastern Polynesia," and (e) indigenous (native but not endemic).

Characteristics of the islands and correlation coefficients with the native species

Endemic species

All endemic species were strongly correlated with island area and the highest elevation of the islands (Table 2). The endemic species of eastern Polynesia were correlated with both the distance to the nearest similar island ($r^2 = 0.291$, $p < 0.01$) and distance to the cyclonic alley (inverse correlation, $r^2 = 0.194$, $p < 0.05$). I did not observe any significant correlation between the endemic species and the other characteristics (Table 2).

Indigenous species

The island area and highest elevation were strongly correlated with the indigenous species richness on the islands (Figure 6(a)–(b)). Then, the results showed inverse correlations between the indigenous species and both distance to the cyclonic alley

Table 2. Correlation between the characteristics of the islands and the endemic species on the 22 volcanic high islands of French Polynesia and Pitcairn (Spearman's correlation coefficients).

Characteristics of the high islands ($n = 22$)	Endemic species			
	Insular	Archipelago	French Polynesia	Eastern Polynesia
Area (km²)	0.53*	0.92**	0.84**	0.54**
Highest elevation (m)	0.58**	0.86**	0.77**	0.45*
Distance to nearest continent (km)	0.15	−0.23	0.05	0.20
Distance to nearest similar island (km)	0.37	−0.14	0.12	0.54**
Distance to nearest archipelago (km)	0.03	0.21	0.05	0.11
Index of isolation (remoteness UNEP)	0.27	−0.07	0.09	0.40
Distance to Tahiti (km)	−0.00	−0.27	−0.37	−0.27
Distance to cyclonic alley (km)	−0.11	0.00	−0.20	−0.44*

*$0.01 \le p \le 0.05$, **$p < 0.01$.

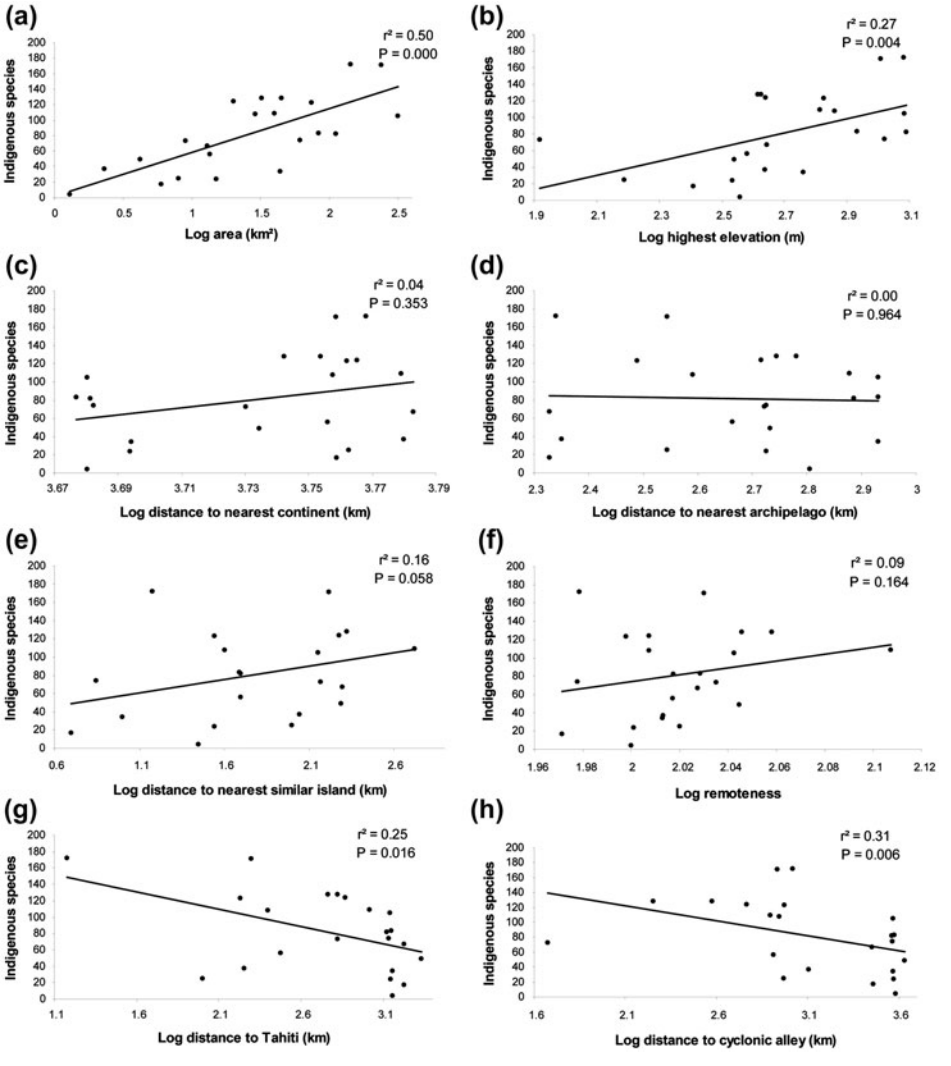

Figure 6. (a–h) Indigenous species richness compared to the characteristics of the 22 high islands with: (a) island area, (b) highest elevation, (c) distance to the nearest continent, (d) distance to the nearest archipelago, (e) distance to the nearest similar island, (f) isolation, (g) distance to Tahiti, and (h) distance to the cyclonic alley.

($r^2 = 0.311$, $p < 0.01$) and distance to Tahiti ($r^2 = 0.256$, $p < 0.05$), (Figure 6(g)–(h), respectively). No correlation was found between the indigenous species and the distances to the nearest continent, nearest archipelago, nearest similar island, and isolation (Figure 6(c)–(f)).

Discussion

Which factors influence native plant diversity?

On the 22 remote volcanic high islands, the number of endemic and indigenous species was strongly related to island area and highest elevation (Table 2 and Figure 5 (a)–(b)).

These results are in agreement with previous studies, which demonstrated that island area and highest elevation are both important predictors for plant diversity on remote islands (Ackerman et al., 2007; Hamilton et al., 1963; Johnson & Raven, 1973; McMaster, 2005). Largest and highest islands harbor more habitat diversity and tend to contain more native species, and vice versa. This species–area relationship may be explained by the theory of insular biogeography and confirms the importance of (1) area effects with limited ecological niche capacity, habitat diversity, and heterogeneity, and (2) fluctuation of the equilibrium between the rate of immigration and extinction (MacArthur & Wilson, 1967; Morand, 2000; Ricklefs & Lovette, 1999; Triantis et al., 2003; Whittaker & Fernández- Palacios, 2007).

Conversely, whereas isolation explains why remote islands support fewer species, possibly due to lower immigration rates and a poor rescue (MacArthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007), no statistically significant correlation was found between native plant diversity and isolation for the 22 islands studied (Table 2 and Figure 6(f)). There is no doubt that the islands of French Polynesia and Pitcairn are among the most remote in the world (Table 1). However, isolation effects (e.g. lower species immigration with increasing distance from the continent) could be tempered by other factors such as inherent differences in plant dispersibility (Daehler, 2006), or a stepping-stone-island effect, which represents the capacity of a large island to increase considerably the flow of propagules to nearby islands (e.g. MacArthur & Wilson, 1967; McMaster, 2005). I observed an inverse correlation between the indigenous species richness on the islands and the distance to Tahiti ($r^2 = 0.256$, $p = 0.016$; Figure 6(g)). This result demonstrates that the biggest and highest island of Tahiti influences the spatial distribution of indigenous species in the islands. Consequently, the large island of Tahiti can be viewed as a "stepping-stone island" and a provider of native species to the surrounding islands in a remote environment.

How can the relationship between native plant diversity and distance to the cyclonic alley be explained?

Whereas endemic species tend to lose their dispersion capacity with time on remote islands (Carlquist, 1974; Florence, 1997), I observed an inverse correlation between endemic species at the eastern Polynesia level and DCA, even though this correlation was weak (Table 2). These endemic species have spread in the Cook Islands, French Polynesia, and the Pitcairn group, and cyclones could play a role in the spatial distribution of these species in the geographic region of eastern Polynesia.

More important, the indigenous species richness was inversely related to the distance to the cyclonic alley, showing that species richness in the islands decreases with the increasing distance to the cyclonic alley (Figure 6(h)). Indigenous species on the islands of French Polynesia and the Pitcairn group mainly originate from the Indo-Malayan Peninsula located to the northwest of the islands studied (Van Balgooy, 1993) and it is commonly accepted that the decrease in species richness from west to east on the Pacific islands is mainly linked to the increasing distance of the remote islands from the mainland source pool of Indo-Malayan and Austro-Melanesian regions (Dahl, 1980, 1984; Ellison, 2009; Van Balgooy, 1993; Van Balgooy, Hovenkamp, & van Welzen, 1996). Data on native plant dispersibility for the study area (Florence, 1997, 2007; Florence, Waldren, & Chepstow-Lusty, 1995; Kingston, 2001) show that anemochory for native species represents 46% in the Austral and 50% in the Society Islands, vs. 43, 34, and 19%, in the Marquesas, Gambier, and Pitcairn group, respectively (Table 3).

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Table 3. Native species and dispersal mechanisms in the archipelagos of French Polynesia and the Pitcairn group (adapted from Florence, 1997, 2007; Florence et al., 1995; Kingston, 2001).

Archipelagos	Native plant species richness	Native species (%)		Dispersal mechanisms of native plants (%)					Mean distance from the cyclonic alley (km)
		Endemic	Indigenous	Undetermined	Autochory	Hydrochory	Zoochory	Anemochory	
Austral	421	20	80	3	1	17	33	46	394
Society	553	40	60	1	2	7	40	50	965
Gambier	83	8	92	4	1	28	33	34	2863
Marquesas	321	48	52	2	1	8	46	43	3213
Pitcairn group	147	13	87	0	0	47	34	19	4281

Considering that indigenous species represent the greatest percentage of native plants in the archipelagos cited above (Table 3), data on dispersal mechanisms for native plants chiefly provide a picture of indigenous dispersion.

The propagules of wind-dispersed species in eastern Polynesia would have had to move against the easterlies above the Pacific Ocean in order to disperse by anemochory from the mainland source pool to eastern Polynesia. Some authors have suggested that wind-dispersed species reached the islands by using the high jet stream blowing from west to east above the easterlies (Carlquist, 1974; Drake, 1992; Florence, 1997, 2007) or during the Quaternary glaciations and strong *El Niño* events when the easterlies were reversed (i.e. blowing from west to east, Wright, Yong, Dawson, Whittaker, & Gardner, 2000). Here, I identify a complementary possibility to explain the long-distance dispersal of native plants in the eastern Pacific basin. Indeed, several authors identified main trajectories of contemporary cyclones in this region, moving from northwest to southeast (Etienne, 2012; Larrue & Chiron, 2010; Woodroffe & Stoddart, 1992), which are congruent with the direction of native species dispersal. Moreover, native plants on the archipelagos situated close to the cyclonic alley tend to record a higher level of plant dispersibility by anemochory than those far away from the cyclonic alley (Table 3). Cyclones are temporal disturbances that interact only during short time spans on islands, but the location of islands in respect to the pathway of disturbances has to be taken into account at the global scale to better understand the spatial pattern of native species within islands. This result is in agreement with the hierarchical theory of species diversity, which considers that diversity is driven by a combination of phenomena occurring at various spatiotemporal scales (Whittaker et al., 2001).

Conclusion

On the remote high volcanic islands studied, native plant diversity is firstly related to island area and the highest elevation. As reported by many authors, this confirms that the elevation and size of the islands are important predictors for native plant diversity on the remote tropical islands. Here, distance to the cyclonic alley clearly contributed to explain native species richness.

It was demonstrated that the geographical distance to the cyclonic alley was an important predictor of the spatial pattern of the indigenous species on the islands. Furthermore, no correlation between native plant diversity and isolation of the islands was found, possibly due to both the stepping-stone-island effect of Tahiti, and a cyclonic-transport-flow effect of distance to the cyclonic alley. Indeed, cyclonic winds may be able to disperse seeds from the mainland source pool to the islands surveyed. These findings suggest that cyclones can increase native species richness in extreme remote islands by increasing the flow of propagules from the source pool region to the remote islands located close to the cyclonic alley, thus reducing the "distance" of the islands to the mainland source pool.

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