Rarity patterns of woody plant species are associated with life form and diversification rates in Pacific islands forests

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PREMISE: Rarity is a complex and central concept in ecology and conservation biology. Yet, it is still poorly understood why some species are rare and others common. Here, we aimed to understand the drivers of species rarity patterns in woody plant communities.

METHODS: We analyzed the local abundance and landscape frequency of 121 woody plant species across 238 plots on American Samoa and Hawaiian islands. We first assessed whether taxonomy, life form (shrub, small tree, large tree), and dispersal syndrome (dispersed by animals or by other means) are associated with the rarity of species. We then analyzed phylogenetic patterns in plant rarity and tested whether rarity patterns are associated with species evolutionary distinctiveness and the number of species within genera and families.

RESULTS: Large trees were less abundant but more frequent than shrub species. Animal-dispersed species tended to be less abundant than species dispersed by other means, while species frequency was not associated with dispersal syndromes. Relative frequency in Hawai'i exhibited a more robust phylogenetic signal than did abundance. Both evolutionary distinctiveness and taxa species richness were significantly associated with the frequency of shrub species in Hawai'i.

CONCLUSIONS: Life form appears consistently associated with the rarity of species. High diversification rate is probably a key factor explaining landscape-scale rarity of native species on isolated archipelagos like Hawai'i. At the landscape scale, rarity appears to be inversely associated with evolutionary distinctiveness, but at the local scale, species abundance may be not associated with evolutionary distinctiveness.

KEY WORDS commonness; dispersal; evolutionary distinctiveness; functional traits; phylogeny; plant size; rarity; speciation; shrubs; trees.

Rarity is a complex and central concept in ecology and conservation biology. The rarity of species can be defined along multiple axes and at different scales, e.g., abundance at the local or community scale, frequency of occurrence at the landscape or habitat scale, and geographic range and niche (or habitat) breath at the regional to global scale (Preston, 1948; Rabinowitz et al., 1986; Kunin and Gaston, 1993, 1997). Species with low local abundance or frequencies, or small geographical range sizes or niche breadths, are likely to be more susceptible to demographic or environmental extinction drivers (e.g., Matthies et al., 2004; Burns and Neufeld, 2009; Staude et al., 2020). Understanding the drivers of species rarity patterns is therefore recognized as an important issue in ecology and conservation biology.

The multiple axes of rarity typically correlate with each other. For example, locally rare species often are less frequent on a landscape scale and have smaller geographical range sizes and niche breadths on a regional scale (Price and Wagner, 2004; Davidar et al., 2008; Arellano et al., 2015). Rare species are therefore likely to be rare at all local, landscape, and regional scales, which compounds extinction risk. However, large variation exists around those broad trends (i.e., locally rare species can be common at landscape or regional scales and vice versa), and factors driving rarity may differ across spatial scales.

Many studies have shown that species ecological traits, notably those related to plant size and dispersal, affect the rarity/commonness patterns of plant species (e.g., Rabinowitz, 1978; Kunin and Gaston, 1993; Kelly et al., 1996; Murray et al., 2002; Price and Wagner, 2004; Kolb et al., 2006; Boulangeat et al., 2012; Arellano et al., 2015; Umaña et al., 2015; Davidar et al., 2018; van der Sande et al., 2020). However, the nature of the relationships between

plant traits and rarity/commonness patterns varies considerably depending on the studied life forms (e.g., grasses, shrubs, or trees) and ecosystems (e.g., Murray et al., 2002). In tropical woody plant communities, taller species tend to have larger geographical range sizes (Dexter and Chave, 2016) than shorter species, while animal-dispersed species tend to be less frequent and abundant (Davidar et al., 2018) and have smaller geographical range sizes (Kelly et al., 1994) than species dispersed by other means.

Rarity may exhibit a phylogenetic signal. Phylogenetically related species tend to resemble each other more than less-related species (e.g., Blomberg et al., 2003; Münkemüller et al., 2012), such as with functional traits (e.g., Swenson et al., 2007; Cornwell et al., 2014; Coelho de Souza et al., 2016). Thus, if rarity of species is related to species traits, closely phylogenetically related species should also exhibit similar rarity/commonness patterns. The analysis of the variation of rarity across the phylogenetic tree has the potential to provide new insights into the drivers of rarity in species-rich ecosystems such as tropical forests, where measuring multiple traits on numerous species is challenging (e.g., Loza et al., 2017).

In addition to the position of taxa in the phylogenetic tree, rarity/commonness patterns are likely associated with taxon size and rate of diversification. Several studies have shown that, at different taxonomic scales (i.e., genus, family, lineages), species belonging to species-rich taxa tend to be rarer (i.e., locally less abundant, smaller geographical range size and/or niche breadth) than species belonging to taxa with fewer species (Schwartz and Simberloff, 2001; Price and Wagner, 2004; Domínguez Lozano and Schwartz, 2005; Dexter and Chave, 2016; Davidar et al., 2018; Fernández-Palacios et al., in press, but see Ricklefs, 2010). Further, Davies et al. (2011) showed that there is a phylogenetic signal in species extinction risk and that extinction risk tends to cluster in species-rich taxa. The proposed mechanism for this is that with high diversification, there will be proportionately high levels of rare and restricted species which are, by definition, more prone to local extinction processes (Schwartz and Simberloff, 2001).

The drivers of species rarity/commonness patterns on island systems have been less explored than on continental systems. Island geography (the area and isolation of the islands) is likely to play an important role in shaping rarity/commonness patterns through its effect on rate of diversification. Higher diversification rates are indeed expected on more isolated and larger islands due to lower colonization rates and higher levels of environmental diversity (Whittaker et al., 2008). Potentially lower dispersal abilities on more isolated islands (Carlquist, 1965, 1966; Ottaviani et al., 2020) may also contribute to higher diversification rates. A strong relationship between taxon diversity and species rarity/commonness patterns is expected on islands, especially in isolated archipelagos because of potentially higher diversification rates (Losos and Ricklefs, 2009).

Here, we studied variations in local abundance and landscape frequency among woody plant species growing in wet forests of the Samoan and Hawaiian tropical Pacific archipelagos. We first tested the predictions (1) that species local abundance and landscape frequency are correlated, and (2) that these two axes of rarity are associated with size (shrub, small tree, or large tree) and dispersal syndrome (dispersed by animals or by other means) of species. We predicted that larger species would be less abundant but more frequent than smaller species and that species dispersed by animals would be less abundant and less frequent than species dispersed by other means. We then tested the hypotheses that (1) groups of closely related species exhibit similar rarity/commonness patterns,

and that (2) species belonging to species-rich taxa are less frequent than species belonging to species-poor taxa because they share the landscape with closely related species. We also expected that higher diversification rates on the Hawaiian islands, which are larger and more isolated than the American Samoan islands, might result in higher levels of rarity for individual species.

MATERIALS AND METHODS

Study sites and vegetation surveys

We analyzed variation in species local abundance and landscape frequency across 0.1-ha plots (20 × 50 m) in four United States National Parks, on five islands and two archipelagos (Table 1, Fig. 1; for plot location, see Appendix S1). The studied islands were all formed above volcanic hotspots but differ in age, size, and isolation. In Hawaiʻi, the hotspot is currently located southeast of the island of Hawaiʻi and island age increases from southeast to northwest (Neall and Trewick, 2008). In American Samoa, the hotspot is located east of the island of Taʻū, and island age increases from east to west (McDougall, 2010). The Hawaiian islands are much larger but more isolated than the islands of American Samoa. Indeed, although the Hawaiian and Samoan islands are about the same distance from the nearest continent (~4100 km west of North America and 3900 km east of Australia, respectively), the Samoan islands are better connected to Australia and Papua New Guinea due to the presence of the Melanesian islands (Fig. 1; Keppel et al., 2009).

Vegetation surveys were conducted between 2010 and 2018 in the most intact wet forests within the parks (Ainsworth et al., 2011). Mean annual precipitation ranged between 1250–8200 mm and 3350–6400 mm and mean annual temperature ranged between 12–20°C in plots in Hawaiʻi and 23–27°C in plots in American Samoa (PRISM gridded climatic data, PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 4 February 2004). Woody plants were recorded in different subplots within each plot according to life form. Prior to sampling, species were designated as shrubs or trees according to the literature (Wagner et al., 1999; Whistler, 2004). At each plot, all shrubs ≥0.5 m tall were recorded in a 2 × 50 m subplot regardless of size class. Large trees with a stem diameter ≥10 cm at ~1.4 m above the base (DBH) were recorded in the entire 20 × 50 m plots and small trees (1 cm ≥ DBH < 10 cm) were recorded in a 10 × 25 m subplots.

Non-native species are widespread in the studied parks (Ibanez et al., 2019) and can affect rarity/commonness patterns (e.g., Hughes et al., 2012). Therefore, we excluded from analysis all plots in which >50% of all recorded individuals were non-native, or in which >25% of the large tree individuals were non-native. The final data set encompassed 238 plots; 172 plots in Hawaiʻi (92 on the island of Hawaiʻi, 35 on Maui, and 45 on Molokaʻi), and 66 plots in American Samoa (41 on Tutuila and 25 on Taʻū). The proportion of non-native woody plants in the studied plots remained particularly high in American Samoa (Appendix S2) because of the presence of two non-native shrubs (*Clidemia hirta*, Melastomataceae; *Cordyline fruticosa*, Asparagaceae) in most of the plots.

Life form and dispersal syndrome

After sampling, species designated as trees were re-classified as large trees if any measured individual belonging to that species was

TABLE 1. Studied national parks and plots surveyed in Hawaiʻi and American Samoa.

Archipelago	Park (Code)	Island	Island area (km²)	Island age (Ma)	No. of plots	No. of species	Elevation (m a.s.l.)
Hawaiʻi	Hawaiʻi Volcanoes (HAVO)	Hawaiʻi	10458	0–0.50	99	31	685–1930
	Haleakala (HALE)	Maui	1888	0.75–1.32	37	35	740–2190
	Kalaupapa (KALA)	Molokaʻi	676	1.75–1.90	45	19	930–1240
American Samoa	National Park of American Samoa (NPSA)	Taʻū	44	0.02–0.07	28	48	325–595
		Tutuila	140	1.00–1.53	44	63	65–385

≥10 cm DBH or as small trees if not. A total of 69 native woody plant species were recorded in American Samoa (62 large trees, 5 small trees, and 2 shrubs) and 52 in Hawaiʻi (20 large trees, 9 small trees, and 23 shrubs). No native species occurred in both Hawaiʻi and American Samoa. Small tree and shrub species were grouped to analyze the effects of life form on species rarity. In Hawaiʻi, the canopy was largely dominated by *Metrosideros polymorpha* (Myrtaceae) (on average 72, 76, and 81% of the large trees on the islands of Hawaiʻi, Maui, and Molokaʻi, respectively). The canopy was more diverse in American Samoa with the most abundant species representing on average only 27% and 29% of the large trees on the islands of Taʻū (*Syzygium samoense*, Myrtaceae) and Tutuila (*Myristica inutilis*, Myristicaceae). Dispersal syndrome, i.e., dispersed by animals (mostly birds or *Pteropus* spp. bats in American Samoa and birds in Hawaiʻi), or by other means (e.g., by wind, water, or gravity), was determined using fruit and seed morphologies as well as information from literature (Wagner et al., 1999; Whistler, 2004). Most recorded species were classified as animal-dispersed (57 species in American Samoa and 48 species in Hawaiʻi), only 12 species in American Samoa and four in Hawaiʻi were classified as dispersed by other means.

Phylogeny and evolutionary distinctiveness

We used a megaphylogeny of vascular plants and the V.PhyloMaker R package (Jin and Qian, 2019) to generate phylogenies of woody plant species. The evolutionary distinctiveness of species (sensu Isaac et al., 2007) was computed using the evol.distinct function from the picante R package (Kembel et al., 2010). Each branch of the phylogenetic tree received a value equal to the branch length divided by the number of descendent species. The distinctiveness of a given species was calculated as the sum of all values for the branches from which it descended. We computed the evolutionary distinctiveness of species for each island and archipelago separately and from phylogenies representing only the species recorded in the surveyed vegetation. We used Spearman's correlation tests to evaluate the association between the evolutionary distinctiveness of a species and the richness of the taxa to which it belonged (i.e., the number of species belonging to its genus and family).

Local abundance and landscape frequency

For each native species, we computed its mean relative abundance and relative frequency on each island and archipelago. The mean relative abundance of species was computed as the mean of the ratio between the number of individuals of a species found in the plot and the total number of individuals for all species inventoried in the plot. For large tree species, the number of individuals inventoried in the plot included both the number of individuals ≥10 cm DBH and the number of individuals in the smaller class sizes. Only the plots where species occurred were averaged. The number of small trees and shrubs sampled in subplots was extrapolated to the full plots. Relative frequency was computed as the ratio between the number of plots where a species occurred (in any of the size classes) and the total number of plots located on the island. We computed the mean relative abundance and the mean relative frequency at the archipelago scale by averaging the island scale mean relative abundance and relative frequency (considering only the islands where species have been recorded).

Analysis

All analyses were performed using R 4.0.2 (R Core Team, 2020) and performed separately for each island and each archipelago. Relative abundance and frequency data were log-transformed for normality.

Relationships between the relative abundance and frequency—We used major axis regression (sma function of the smatr 3 R package; Warton et al., 2012) to test the relationships between the relative abundance and frequency of species across life forms (large trees vs small trees or shrubs) and dispersal syndromes (dispersed by animal or by other means). To our knowledge phylogenetic non-independence between species cannot be taken into account when fitting major axis regression. We therefore tested for phylogenetic dependence in models' residuals using Pagel's λ.

Phylogenetic signal—Following Münkemüller et al. (2012), phylogenetic signals in relative abundance and frequency of species were tested using the Abouheif's C_{mean} (Abouheif, 1999) and Pagel's λ (Pagel, 1999). Note that polytomies and missing branch length information have negligible impacts on those indices (Münkemüller et al., 2012). Abouheif's C_{mean} was computed using the abouheif.moran function of the adephylo R package (Jombart and Dray, 2008), and Pagel's λ was determined using the phylosig function from the phytools R package (Revell, 2012). Abouheif's C_{mean} tests the autocorrelation between tips values, i.e., here species values, and their position in the phylogenetic tree; $C_{mean} = 0$ indicates independence, while $C_{mean} > 0$ indicates that closely related species tend to have similar values. Pagel's λ indicates whether a Brownian motion model of evolution (i.e., trait value changes randomly, in both direction and distance, over any time interval) correctly predicts the pattern of covariance among species values; λ tends toward 0 when species values are independent from the phylogeny, while λ tends toward 1 when species values are in complete agreement with the phylogeny. Phylogenetic signals in species life form (large tree or small tree / shrub) and dispersal syndrome (dispersed by animals or by other means) were tested using D of Fritz and Purvis (2010)
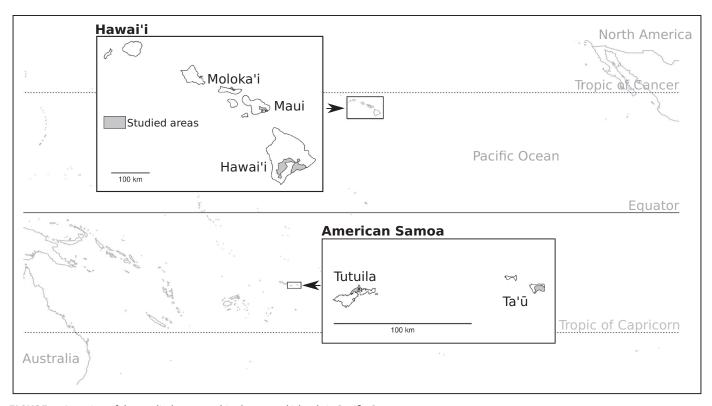
FIGURE 1. Location of the studied areas, archipelagos, and islands in Pacific Ocean.

for binary traits and the phylo.d function from the caper R package (Orme et al., 2018). D tends toward 1 when observed traits are independent from the phylogeny, while D tends toward 0 when traits are in complete agreement with the phylogeny and a Brownian model of evolution. Estimated C_{mean}, λ, and D were tested for the null hypothesis of absence of signal by randomization ($N = 1000$) for C_{mean} and D and by likelihood ratio test for λ.

To analyze and decompose the phylogenetic signals, we estimated the ancestral relative abundance and frequency values at each node using the fastAnc function from the phytools R package (Revell, 2012). Observed values were compared to those obtained after tips randomization with 1000 iterations.

Effects of dispersal syndrome, life form, and evolutionary distinctiveness on species rarity—We used phylogenetic linear models (pgls function from the caper R package) to test whether the relative abundance and frequency of species were associated with their dispersal syndrome, life form, and evolutionary distinctiveness. Phylogenetic linear models can account for phylogenetic non-independence between species. All possible combinations of explanatory variables were tested, and we used likelihood ratio tests to test the significance of the explanatory variables.
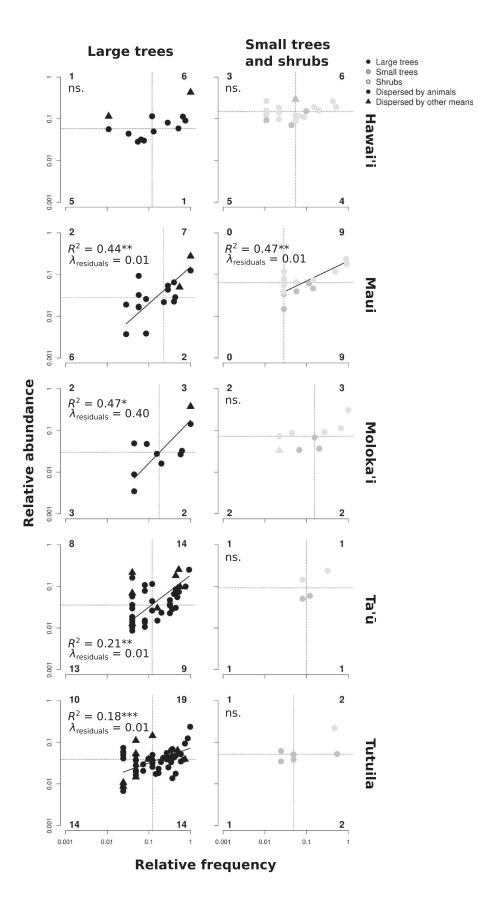
RESULTS

Relationships between the relative abundance and frequency

The strength of the relationship between the two axes of rarity differed between life forms (Fig. 2). The log-transformed relative abundance and frequency of large tree species were positively and linearly related to each other on all islands ($R^2 = 0.18–0.47$, $P < 0.05$), except Hawai'i ($P = 0.100$). In contrast, for small tree / shrub species the relationship was only significant on Maui ($R^2 = 0.47$, $P = 0.0017$).

Phylogenetic signals

We did not find consistent phylogenetic signals for relative abundance, relative frequency, life forms or dispersal syndrome (Table 2). A significant phylogenetic signal in species relative abundance was only detected on Tutuila ($C_{mean} = 0.22$, $P = 0.09$) with higher than expected relative abundance for the magnoliids and the genus *Barringtonia* (Lecythidaceae). Significant phylogenetic signals in dispersal syndromes were detected on Ta'ū and Tutuila ($D = 0.01$ and 0.25, $P = 0.020$ and 0.016, Table 2 and Fig. 3) and at the archipelago scale ($D = −0.03$, $P = 0.003$, see Appendix S3).

FIGURE 2. Relationship between the relative abundance and frequency of woody plant species across the islands of American Samoa and Hawai'i. Only significant trend lines (i.e., $p \leq 0.05$, with *$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$) are shown. Horizontal and vertical dotted lines represent median values. Bold numbers on each corner of the plots represent the number of species found in each category (i.e., relative low abundance and frequency, lower left corner, relative low abundance and high frequency, lower right corner, relative high abundance and low frequency, upper left corner, and relative high abundance and frequency, upper right corner). Phylogenetic signal in models' residuals were tested using Pagel's λ.

Large trees

Small trees and shrubs

• Large trees
◔ Small trees
○ Shrubs
● Dispersed by animals
▲ Dispersed by other means

Relative abundance

Hawai'i

ns.

$R^2 = 0.44**$
$\lambda_{residuals} = 0.01$

Maui

$R^2 = 0.47**$
$\lambda_{residuals} = 0.01$

$R^2 = 0.47*$
$\lambda_{residuals} = 0.40$

Moloka'i

ns.

$R^2 = 0.21**$
$\lambda_{residuals} = 0.01$

ns.

Ta'ū

$R^2 = 0.18***$
$\lambda_{residuals} = 0.01$

ns.

Tutuila

Relative frequency

TABLE 2. Phylogenetic signal in log-transformed relative abundance, and frequency (Abouheif's C_{mean}, Pagel's λ) and in life form, dispersal syndrome (Fritz and Purvis' D). Values in bold represent significant phylogenetic signal (*$P \leq 0.05$, **$P \leq 0.01$).

Archipelago	Island	Relative abundance		Relative frequency		Life form	Dispersal syndrome
		C_{mean}	λ	C_{mean}	λ	D	D
Hawai'i	Hawai'i	−0.04	0.01	0.15	0.52	0.77	0.01
	Maui	0.12	0.2	0.08	0.09	0.76	−0.1
	Moloka'i	−0.12	0.01	0.06	0.14	0.65	2.09
	Archipelago	0.15	0.01	**0.16***	0.27	**0.56***	0.56
American Samoa	Ta'ū	0.13	0.38	0.01	0.01	0.84	**0.01***
	Tutuila	**0.22****	0.40	0.04	0.02	0.88	**0.25***
	Archipelago	0.05	0.21	−0.02	0.01	0.76	**−0.03****

Significant phylogenetic signals were found for species relative frequency ($C_{mean} = 0.16$, $P = 0.050$) and life forms ($D = 0.56$, $P = 0.020$) in the Hawaiian archipelago (Table 2 and Fig. 4), although no signal was found at the islands scale (Appendix S4). Higher than expected relative frequencies were found for the asterids, and within them the Ericales (+ *Broussaisa arguta*, Hydrangeaceae) and the campanulids. This last pattern was driven by *Ilex anomala* (Aquifoliaceae) and *Cheirodendron trigynum* (Araliaceae) occurring in 75% and 65% of plots, respectively. In contrast, within the campanulids, the common ancestor of *Cyanea* spp., *Clermontia* spp., and *Trematolobelia* spp. (i.e., all inventoried Campanulaceae exept *Lobelia gloriamontis*), exhibited significantly lower than expected relative frequency.

***Effects of dispersal syndrome, life form, and evolutionary distinctiveness on species rarity*—**Dispersal syndromes and life forms had consistent associations with the relative abundance of species across the studied islands and archipelagos (Table 3; Appendix S5). Animal-dispersed species were less abundant than species dispersed by other means and large tree species were less abundant than small tree / shrub species. These effects were significant on all islands except Moloka'i. Life forms had also a consistent effect on the relative frequency of species across the studied islands and archipelagos with large tree species tending to be more frequent than small tree / shrub species (Table 4; Appendix S6). However, this effect was only significant for the Hawaiian archipelago and within it on the islands of Hawai'i and Maui.

As expected, the evolutionary distinctiveness of a species was strongly and negatively correlated to the number of species belonging to the same genus or family (see Appendix S7). The evolutionary distinctiveness of species did not have a consistent effect on the relative abundance of species. Indeed, it only had a significant effect on the abundance of species on the island of Hawai'i when added to the effects of life forms (more evolutionarily distinct species were more abundant). The evolutionary distinctiveness of species had a consistent positive effect on the frequency of species on the Hawaiian islands, but this effect was only marginally significant at the archipelago scale ($P = 0.062$).
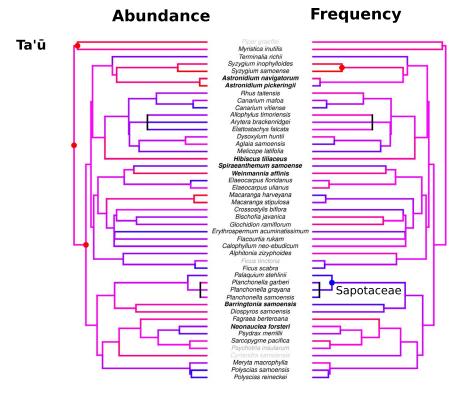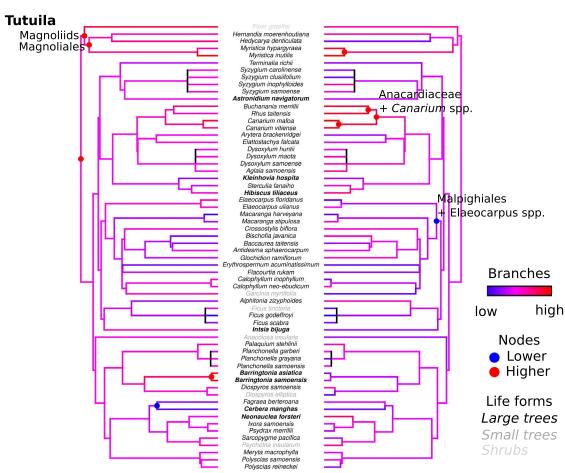
DISCUSSION

Local abundance

We found that life form was associated with species local abundance. Small tree and shrub species were more abundant than large

tree species on all studied islands, although this relationship was not significant in Moloka'i. This result may be explained by the negative relationship between the size of species and their relative abundance, likely due to competition for space and resources (e.g., Westoby, 1984; Enquist and Niklas, 2001; White et al., 2007). Within the relatively small plots we studied (0.1 ha), there is more room for small trees or shrubs growing in the understory than for large trees competing for light and space in the canopy. Our results, however, contrast with those of Arellano et al. (2015) in Bolivian tropical Andes who found small trees less abundant than large trees. This opposite pattern may be explained by different threshold values used in plant inventories. Those authors excluded small trees <2.5 cm DBH, while we excluded small trees <1 cm DBH. As we observed, small tree species are more common in smaller size classes and excluding individuals <2.5 cm DBH excluded species that seldom reach such size.

Similar to Davidar et al. (2018) in Western Ghats of India, we found that species dispersed by animals tended to be less abundant than species dispersed by other means. Dispersal syndrome alone has only a significant effect on relative abundance on the island of Hawai'i, but adding dispersal syndrome to the effects of life form improved the models explaining species abundance on all islands except Moloka'i. When present, the relatively high abundance of non-animal-dispersed species likely reflect the recruitment of fast-growing, light-demanding species, after canopy opening by disturbances such as tropical cyclones (e.g., Webb et al., 2011). The relationship between dispersal syndrome and species rarity may have been underrepresented because only a few of the species in this study were dispersed by wind and most of these species were large trees.

Strong phylogenetic signals for species local abundance were not observed on the studied islands, suggesting that in the studied ecosystems, the local abundance of species was either (1) not affected by species traits or (2) affected by traits that do not exhibit strong phylogenetic signals. For instance, life forms and dispersal syndrome exhibited weak phylogenetic signals. Contrary to our expectation, the local abundance of species did not correlate with their evolutionary distinctiveness. Evolutionary distinctiveness had only a significant effect on the relative abundance of species in Hawai'i when added to the effect of life form. Results from Mi et al. (2012) suggest that the sign and the strength of the relationship between local abundance and evolutionary distinctiveness could be highly site-dependent. Notably, locally rare species could be more evolutionarily distinct than common species in gap-dominated forests (in which forest dynamic is mainly driven

FIGURE 3. Phylogeny of the species of Ta'ū and Tutuila (American Samoa) with branches colored according to species abundance (left tree) and species frequency (right tree). Species highlighted in bold font are not dispersed by animals. Blue or red points highlight nodes where the common ancestor have significantly lower or higher values, respectively, than expected under tip randomization model, i.e., values inferior (superior) to the quantile 2.5% (97.5%) from 1000 iterations.
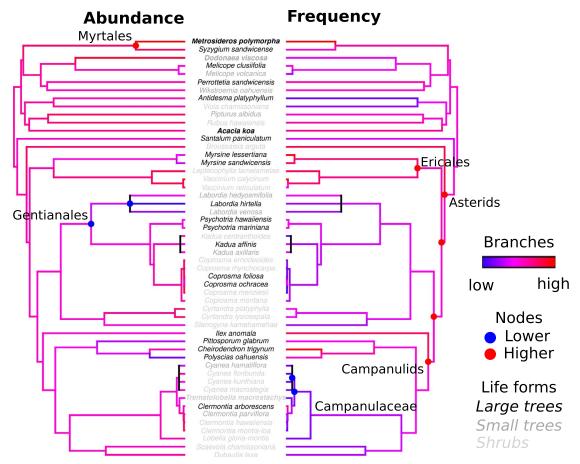
Abundance

Frequency

Ta'ū

Piper graeffei
Myristica inutilis
Terminalia richii
Syzygium inophylloides
Syzygium samoense
Astronidium navigatorum
Astronidium pickeringii
Rhus taitensis
Canarium mafoa
Canarium vitiense
Allophylus timoriensis
Arytera brackenridgei
Elattostachys falcata
Dysoxylum huntii
Aglaia samoensis
Melicope latifolia
Hibiscus tiliaceus
Spiraeanthemum samoense
Weinmannia affinis
Elaeocarpus floridanus
Elaeocarpus ulianus
Macaranga harveyana
Macaranga stipulosa
Crossostylis biflora
Bischofia javanica
Glochidion ramiflorum
Erythrospermum acuminatissimum
Flacourtia rukam
Calophyllum neo-ebudicum
Alphitonia zizyphoides
Ficus tinctoria
Ficus scabra
Palaquium stehlinii
Planchonella garberi
Planchonella grayana
Planchonella samoensis
Barringtonia samoensis
Diospyros samoensis
Fagraea berteroana
Neonauclea forsteri
Psydrax merrilii
Sarcopygme pacifica
Psychotria insularum
Cyrtandra samoensis
Meryta macrophylla
Polyscias samoensis
Polyscias reineckei

Sapotaceae

Tutuila

Magnoliids
Magnoliales

Piper graeffei
Hernandia moerenhoutiana
Hedycarya denticulata
Myristica hypargyraea
Myristica inutilis
Terminalia richii
Syzygium carolinense
Syzygium clusiifolium
Syzygium inophylloides
Syzygium samoense
Astronidium navigatorum
Buchanania merrilii
Rhus taitensis
Canarium mafoa
Canarium vitiense
Arytera brackenridgei
Elattostachys falcata
Dysoxylum huntii
Dysoxylum maota
Dysoxylum samoense
Aglaia samoensis
Kleinhovia hospita
Sterculia fanaiho
Hibiscus tiliaceus
Elaeocarpus floridanus
Elaeocarpus ulianus
Macaranga harveyana
Macaranga stipulosa
Crossostylis biflora
Bischofia javanica
Baccaurea taitensis
Antidesma sphaerocarpum
Glochidion ramiflorum
Erythrospermum acuminatissimum
Flacourtia rukam
Calophyllum inophyllum
Calophyllum neo-ebudicum
Garcinia myrtifolia
Alphitonia zizyphoides
Ficus tinctoria
Ficus godeffroyi
Ficus scabra
Intsia bijuga
Anacolosa insularis
Palaquium stehlinii
Planchonella garberi
Planchonella grayana
Planchonella samoensis
Barringtonia asiatica
Barringtonia samoensis
Diospyros samoensis
Diospyros elliptica
Fagraea berteroana
Cerbera manghas
Neonauclea forsteri
Ixora samoensis
Psydrax merrilii
Sarcopygme pacifica
Psychotria insularum
Meryta macrophylla
Polyscias samoensis
Polyscias reineckei

Anacardiaceae
+ *Canarium* spp.

Malpighiales
+ *Elaeocarpus* spp.

Branches

low   high

Nodes

● Lower
● Higher

Life forms
Large trees
Small trees
Shrubs

FIGURE 4. Phylogeny of Hawaiian species with branches colored according to species abundance (left tree) and species frequency (right tree). Species highlighted in bold font are not dispersed by animals. Blue or red points highlight nodes where the common ancestor have significantly lower or higher values, respectively, than expected under tip randomization model, i.e., values inferior (superior) to the quantile 2.5% (97.5%) from 1000 iterations.

by old trees that die and fall forming small openings or gaps) but not in disturbance-dominated forests (in which forest dynamic is mainly driven by frequent large openings caused by disturbances) such as American Samoa (e.g., tropical cyclones; see Webb et al., 2011, 2014) and Hawaiʻi (e.g., lava flows, canopy die-back, or tropical cyclones; see Mueller-Dombois and Fosberg, 1998). The independence between the local abundance and evolutionary distinctiveness in disturbance-dominated forests might be explained by a loss of functionally distinct species (Umaña et al., 2017).

Landscape frequency

We found that life form was also associated with species frequency. Shrub and small-tree species were consistently less frequent than large tree species on all studied islands. However, this relationship was only significant in the archipelago of Hawaiʻi and, within this archipelago, only on the islands of Hawaiʻi and Maui. We also found a significant phylogenetic signal in the frequency of species in Hawaiʻi. Our results suggest that this signal was driven by different diversification rates and different number of species per taxa across the phylogenetic tree. The frequency of species in Hawaiʻi tended to increase with the evolutionary distinctiveness of species. As found in previous studies, species belonging to species-rich taxa

(i.e., which have a low evolutionary distinctiveness) were less frequent than species belonging to species-poor taxa (Schwartz and Simberloff, 2001; Price and Wagner, 2004; Domínguez Lozano and Schwartz, 2005; Dexter and Chave, 2016; Davidar et al., 2018; Fernández-Palacios et al., in press).

The Hawaiian Lobelioidae (Campanulaceae) is one of the foremost examples of diversification on islands with 125 species originating from a single colonization event (Givnish et al., 2009; Price and Wagner, 2018). High diversification in this lineage has likely been promoted by poor dispersal in the forest understory (Price and Wagner, 2004; Givnish et al., 2009). Ten of the 11 Lobelioidae inventoried in our study were shrubs or small trees present at low relative frequency (1–4% of plots). Only the larger tree species *Clermontia arborescens* was present at a relatively high frequency (27% of plots). In contrast, *Ilex anomala*, another campanuliid and the only native Aquifoliaceae in Hawaiʻi, was 10-fold more frequent than most of the Lobelioidae (>50% of plots).

Beyond the Lobelioidae, shrub or small tree species were globally less frequent than large trees in Hawaiʻi, which provides further support for the hypothesis that shrub species are rarer than tree species on landscape and regional scales (Kelly et al., 1996; Murray et al., 2002). This pattern may be due to better dispersal by larger species compared to smaller species (Thomson et al., 2011). Smaller

TABLE 3. Phylogenetic least-squares (PGLS) regressions examining the effects of dispersal syndromes (abiotic vs biotic), life form (large tree vs small tree or shrub), and the log-transformed evolutionary distinctiveness on the log-transformed relative abundance of species. "+" represents variables with positive effects, "-" variables with negative effects, and "- / +" variables for which the direction of the effects depends on which other variables are in the model. Significant effects (i.e., $P \leq 0.05$) are highlighted in bold and "*" represents variables with significant effects only when they are associated with other variables in the model. For parameter estimates and likelihood ratio tests, see Appendix S5.

Archipelago	Island	Dispersal (biotic)	Life form (small tree or shrub)	Evolutionary distinctiveness
Hawai'i	Hawai'i	-	+	+*
	Maui	-*	+	-
	Moloka'i	-	+	- / +
	All	-*	+	- / +
American Samoa	Ta'ū	-*	+	+
	Tutuila	-*	+	-
	All	-*	+	- / +

life forms such as shrubs are also likely to have shorter generation times, which together with lower dispersal may favor higher diversification rates (Boucher et al., 2017). Loss of native pollinators and dispersers in Hawai'i that particularly affect understory plant species is also likely to increase rarity of Hawaiian shrub / small tree species (e.g., Aslan et al., 2014).

In contrast to the results for Hawai'i, we found no significant phylogenetic signal in the frequency of species in American Samoa. This lack of pattern may be due to lower diversification rates in American Samoa compared to Hawai'i, which is notably illustrated by a much lower endemism rate (30% vs. 90%, respectively). Lower diversification rates are indeed expected on less-isolated and smaller islands due to higher colonization rates and lower levels of environmental diversity (Whittaker et al., 2008). Potentially greater dispersal abilities on less-isolated islands (Carlquist, 1965, 1966; Ottaviani et al., 2020) may also contribute to lower diversification rates in American Samoa compared to Hawai'i. Finally, the phylogenetic signal observed in Hawai'i was driven by highly diversified shrub taxa, while only four shrub species were inventoried in American Samoa.

CONCLUSIONS

We found that life form is a major trait explaining variation in the local abundance and landscape frequency of species. We hypothesize that poor dispersal of shrub species in the forest understory and associated higher diversification rates are likely the main factors explaining landscape-scale rarity for Hawaiian shrub species. The local abundance and landscape frequency we computed only

characterize species rarity pattern in the surveyed areas (i.e., undisturbed tropical wet forests), studied species might exhibit different patterns in other areas (e.g., in cooler, drier, or more disturbed areas, see Price et al., 2012). Lack of significance of the relationship between life form and rarity/commonness patterns of plant species on Molokai'i relative to the other Hawaiian Islands likely results from the relatively small geographic area and small elevation gradient covered by our sampling on this island. On Molokai'i, 45 plots covered a 3-km² area and a 310 m elevational range, while on Maui, 37 plots covered a 17-km² area and a 1450 m elevational range. Despite a larger sample size, fewer species were inventoried on Molokai'i (19 species) than on Maui (35 species). These two islands belong to the Maui Nui complex and have been connected during most of the last 1.2 Ma (Price and Elliott-Fisk, 2004). Species rarity/commonness patterns should therefore be cautiously interpreted in the light of the spatial coverage and intensity of the sampling.

To our knowledge, all studies that have explored phylogenetic patterns in the rarity of woody plants have been conducted on a regional scale, and no comparisons have been conducted between regions in the search of a more general pattern. Our results on Hawai'i support former observations that asterids might be rarer than rosids in woody plant communities (Dexter and Chave, 2016; Loza et al., 2017). Such a general pattern may also be due to asterids being globally of small stature (Cornwell et al., 2014), but exceptions exist such as *Scalesia pedunculata* (Asteraceae), which can dominate forest canopies in the Galapagos archipelago (Itow, 1995). Our comparison between American Samoa and Hawai'i suggests that biogeography and evolutionary history can affect rarity patterns, with large isolated islands being more likely to have higher diversification rates and rarer species than

TABLE 4. Phylogenetic least-squares (PGLS) regressions examining the effects of dispersal syndromes (abiotic vs biotic), life form (large tree vs small tree or shrub), and the log-transformed evolutionary distinctiveness on the log-transformed relative frequency of species. "+" represents variables with positive effects, "-" variables with negative effects, and "- / +" variables for which the direction of the effects depends on which other variables are in the model. Significant effects (i.e., $P \leq 0.05$) are highlighted in bold and "*" represents variables with significant effects only when they are associated with other variables in the model. For parameter estimates and likelihood ratio tests, see Appendix S6.

Archipelago	Island	Dispersal (biotic)	Life form (small tree or shrub)	Evolutionary distinctivness
Hawai'i	Hawai'i	+*	-	+
	Maui	-	-	+
	Moloka'i	+	-	+
	All	-*	-	+
American Samoa	Ta'ū	-	-	+
	Tutuila	+	-	-
	All	+	-	-

smaller or less isolated islands. However, observed differences between rarity/commonness patterns in American Samoa and Hawai'i might also result from differences in the structure, composition, and dynamics of the canopy. For instance, the establishment and growth of small-tree and shrub species might be easier in Hawaiian forest where the canopy is dominated by a shade-intolerant species, *Metrosideros polymorpha* (e.g., Burton and Mueller-Dombois, 1984) that recruits by cohort after large openings (e.g., Mertelmeyer et al., 2019).

Finally, while the importance of conserving evolutionarily distinct species to preserve phylogenetic diversity has long been acknowledged (e.g., Faith, 1992; Isaac et al., 2007; Winter et al., 2013), few studies have explored whether or not evolutionarily distinct species are particularly rare. Our results suggest that evolutionary distinctiveness is poorly associated with local species abundance and that evolutionarily distinct species may be less rare on a landscape scale than less evolutionarily distinct species belonging to species-rich lineages.

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AUTHOR CONTRIBUTIONS

T.I., P.J.H., and J.P.P. conceived the idea, A.A. and J.G. acquired the data, T.I. analyzed the data and wrote the first draft. All authors contributed to interpret the results and write the final manuscript.

DATA AVAILABILITY

All plot data are available on the Integrated Resource Management Application (IRMA) portal of the National Parks Service (https://irma.nps.gov/DataStore/Reference/Profile/2244610). Species relative abundance and frequency are available in the Appendix S8.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Location of the plots in the National Parks.

APPENDIX S2. Proportion of non-native plants in the studied plots.

APPENDIX S3. Phylogeny of the species of American Samoa.

APPENDIX S4. Phylogeny of the species of the islands of Hawai'i, Maui, and Molokai'i.

APPENDIX S5. Phylogenetic least-squares (PGLS) regressions examining the effects of dispersal syndromes (D, abiotic vs. biotic), life form (LF, large tree vs small tree or shrub), and the log-transformed evolutionary distinctivness (ED) on the log-transformed relative abundance of species.

APPENDIX S6. Phylogenetic least-squares (PGLS) regressions examining the effects of dispersal syndromes (D, abiotic vs biotic), life form (LF, large tree vs small tree or shrub), and the log-transformed evolutionary distinctivness (ED) on the log-transformed relative frequency of species.

APPENDIX S7. Sperman's rank correlation r between species distinctivness and the number of the species in genera or families.

APPENDIX S8. Species relative abundance and frequency.

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