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RESEARCH ARTICLE

Diversity responses to precipitation gradients differ between older and younger islands of Hawaiʻi

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Abstract

Studying the interaction between macroevolutionary and ecological factors is critical for understanding the principles of diversity regulation and predicting the effects of human activities. Here, we use the geological chronology of the Hawaiian archipelago as a testbed to examine the interaction between island age and climatic factors (i.e., precipitation) on contemporary patterns of tree taxonomic diversity. To this end, we estimated patterns of tree species diversity from 375 forest plots spread across steep precipitation gradients and different substrate ages on a younger island (Hawaiʻi; ~ 0.5 million years old), an intermediate-aged island (Maui Nui complex; ~ 2 million years old), and an older island (Oʻahu; ~ 3 million years old). We found a clear positive relationship between precipitation and diversity on the oldest island (Oʻahu), but no such relationship on the two younger islands (islands in the Maui Nui complex and Hawaiʻi). We also found high species turnover between drier and wetter environments on the oldest island, which suggests ecological specialization on these habitat types, but not on the younger islands. However, when we included plots that were highly invaded by alien species, the effect varied and precipitation had a larger effect on diversity and turnover on the younger islands. This could be because the younger islands may be more vulnerable to invasions. Our results suggest that the response of diversity to climate variation differs substantially across the Hawaiian Islands, possibly because of differences in the age of the islands; however, biological invasions are degrading this signature.

Highlights

- Local diversity responses to a steep precipitation gradient are stronger on older Hawaiian Islands, likely due to longer timescales for macroevolutionary processes.
- Species turnover to distinct precipitation conditions varies across islands of the Hawaiian archipelago, with older islands exhibiting greater precipitation-driven ecological specialization.
- Alien species alter local diversity responses to precipitation, particularly on the youngest island of the archipelago.
- The presence of alien species is modifying the pattern of species turnover across distinct precipitation conditions, with dry and mesic habitats on intermediate-age islands showing higher species turnover.
- Biological invasions are currently reshaping plant diversity patterns in the Hawaiian archipelago.

Resumen

Estudiar la interacción entre factores macroevolutivos y ecológicos es fundamental para comprender los principios de regulación de la diversidad y predecir los efectos de las actividades humanas. En este estudio, utilizamos la cronología geológica del archipiélago hawaiano como laboratorio natural para examinar la interacción entre la edad de las islas y factores climáticos (específicamente, precipitación) en los patrones contemporáneos de diversidad taxonómica de árboles. Con este fin, estimamos los patrones de diversidad de especies arbóreas a partir de 375 parcelas forestales distribuidas a lo largo de gradientes marcados de precipitación y diferentes edades de sustrato en una isla más joven (Hawai'i; ~0.5 millones de años), una isla de edad intermedia (complejo Maui Nui; ~2 millones de años) y una isla más antigua (Oahu; ~3 millones de años). Encontramos una relación positiva entre la precipitación y la diversidad en la isla más antigua (O'ahu), pero no tal relación en las dos islas más jóvenes (islas del complejo Maui Nui y Hawai'i). También encontramos una alta rotación de especies entre ambientes más secos y más húmedos en la isla más antigua, lo que sugiere especialización ecológica en estos tipos de hábitat, pero no en las islas más jóvenes. Sin embargo, cuando incluimos parcelas que estaban altamente invadidas por especies exóticas, el efecto varió y la precipitación tuvo un mayor impacto en la diversidad y rotación en las islas más jóvenes. Esto podría deberse a que las islas más jóvenes pueden ser más vulnerables a las invasiones. Nuestros resultados sugieren que la respuesta de la diversidad a la variación climática difiere sustancialmente entre las Islas Hawaianas, posiblemente debido a diferencias en la edad de las islas; sin embargo, las invasiones biológicas están degradando estos patrones naturales de diversidad.

Keywords

Alien species, alpha diversity, beta diversity, Hawaiian forest, island ecology, precipitation, taxonomic diversity

Introduction

One of life's most distinctive features is its varied types and forms–collectively known as biodiversity (Wilson 1988; Magurran 2021; Díaz and Malhi 2022). For centuries, ecologists and evolutionary biologists have strived to understand the patterns of biodiversity, and the mechanisms that cause it, for example, across latitudinal gradients (Hillebrand 2004) or across islands of different sizes, ages and levels of isolation (Gillespie and Baldwin 2010; Warren et al. 2015). Most patterns of biodiversity variation can be attributed to a combination of historical biogeography (including macroevolution) and contemporary environmental conditions (e.g., precipitation and temperature) (Brown et al. 2013; Keil and Chase 2019). Today, however, the human footprint can have as great, or greater, influence on biodiversity and can obscure natural patterns of biodiversity variation (Russell and Kueffer 2019; Nogué et al. 2021).

Volcanic islands have long served as a laboratory to study patterns of biodiversity (Whittaker et al. 2017). The Hawaiian archipelago is an example of this (Gillespie 2001; Shaw and Gillespie 2016), as it has been recently formed as part of a hotspot volcanic system that has led to a linear arrangement of islands that successively increases in age (Fig. 1) (Clague 1996). As the archipelago is young, that is, in the early to intermediate stages of island ontogeny (Whittaker et al. 2008; Borregaard et al. 2016), older main Hawaiian Islands maintain high levels of environmental heterogeneity (Barajas-Barbosa et al. 2020) and diversity (Craven et al. 2019). Thus, the environment and geological chronology of the Hawaiian Islands are invaluable to study the evolutionary history of organisms and communities (Baldwin 1997; Gillespie 2004; Givnish et al. 2009) and provide ecologists with a model system in which to study the effect of macroevolutionary time on contemporary ecological processes that shape biodiversity patterns (Craven et al. 2019; Barton et al. 2021).

The older major islands of the Hawaiian archipelago (Kaua'i, O'ahu) have more plant species than the younger islands (Maui, Hawai'i) (Price 2004; Shaw and Gillespie 2016; Lim and Marshall 2017). However, how these diversity patterns are reflected at local scales allowing the possibility to disentangle ecological processes, has only been recently examined. Craven et al. (2019) showed that the older major Hawaiian Islands harbor higher local species diversity than younger islands. Specifically, they found that plots on the older islands of Kaua'i and O'ahu had higher native species diversity locally (and a greater number of rare species) for a given sampling effort, compared to younger islands, particularly the youngest island of Hawai'i. These patterns were obscured, however, when both native and alien species were included in the analyses, suggesting that the introduction of alien species may erode the signature of island age on species diversity. While the analyses of Craven et al. (2019) suggest a macroevolutionary signature on local ecological patterns, they did not examine the interaction between macroevolutionary time and the responses of tree diversity to other environmental factors known to influence diversity, such as rainfall gradients.

Here, we examine patterns of biodiversity in both ecological space along steep precipitation gradients, and across islands with varying geological ages. We take advantage of the particular geography of the Hawaiian archipelago, where each major island experiences dramatic climate variation from very dry to very wet because they abruptly rise from the sea as a mountainous volcano. Specifically, each island has a very wet windward (east) side where the air rises and loses water heading over the volcano in the form of precipitation, and a very dry leeward (west) side of the island (Fig. 1). As a result, each island has a precipitation gradient that can range from about 300 mm/year on the dry side to over 10000 mm/year on the wet side (Fig. 1). In addition, within islands, repeated volcanic eruptions create heterogeneous substrate ages on each island, which can influence local responses of diversity to the environment. Therefore, since precipitation and substrate age are key drivers of plant diversity patterns (Kreft and Jetz 2007), especially for trees (Keil and Chase 2019; Sandel et al. 2020), the Hawaiian islands provide an important testing grounds for examining patterns of species diversity within and across islands.

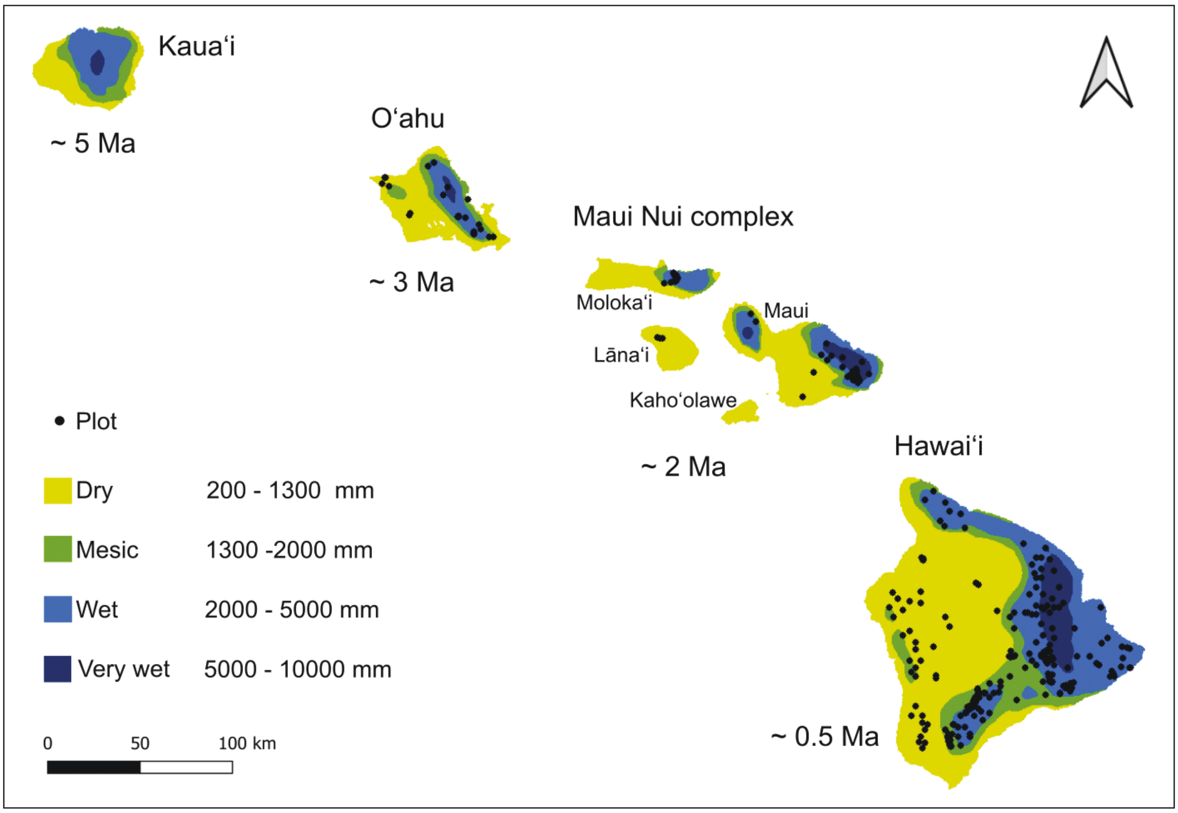

Figure 1. Distribution of rainfall and Open Nahele plots (black dots) across three main islands of the Hawaiian archipelago studied here. The analysis including relatively uninvaded plots (i.e., < 40% individuals of alien species) is composed of 282 plots (Hawai'i Island n = 190, Maui Nui n = 74 and O'ahu Island n = 18). The analysis, including both uninvaded plots and highly invaded plots (> 40% individuals of alien species), is composed of 375 plots (Hawai'i Island n = 254, Maui Nui n = 86 and O'ahu Island n = 35). Rainfall units (mm) are based on mean annual precipitation i.e., mm/year. Island age approximation (Ma) corresponds to million years.

In this study, we expect there to be more species on the older islands (Price 2004; Craven et al. 2019), and more species in wetter than drier regions (Adler and Levine 2007; Esquivel-Muelbert et al. 2017). Although, plant diversity responses to precipitation can be complex and often non-linear, particularly at extreme precipitation levels (> 5000 mm/year) (Whittaker and Heegaard 2003; Korell et al. 2021). We further expect higher species turnover between habitats with different amounts of precipitation than those with similar precipitation (Givnish 1999; Idárraga-Piedrahíta et al. 2022). What is unknown, however, is how island age and precipitation interact and how these potential interactions affect tree diversity. Because there has been more time for the evolution, colonization, and adaptation of precipitation specialists on older islands (Segovia et al. 2020), we ask whether there are stronger responses of local diversity and species turnover along gradients of precipitation on older compared to younger islands. However, because alien species have evolved elsewhere, their presence and distribution would be less constrained by macroevolutionary time on islands that differ in age. As a result, we ask whether including alien species in the analysis of tree diversity patterns and composition along precipitation gradients differs from the patterns observed for the native species and potentially weakens the signal of island and substrate age (Craven et al. 2019). To investigate these patterns, we used sample-controlled analyses of tree diversity data from a database of forest plots (Craven et al. 2018) distributed across the youngest island of Hawai'i (~ 0.5 Ma), the intermediate-aged Maui Nui island complex (~ 2 Ma) and the older island of O'ahu (~ 3 Ma) (Fig. 1), focusing on the relationship between local diversity (i.e., alpha diversity) and turnover across local diversity (beta diversity) with the environment.

Methods

Forest plot data

We used data on tree abundance and composition from forest plots sampled across the major islands of the Hawaiian archipelago using largely similar methods and compiled in the updated version of the Open Nahele database (Craven et al. 2018). We specifically used data from plots that ranged from 100 m^2–10000 m^2 in area and had a minimum of 15 individuals (so that we could use rarefaction-based tools to control for sampling effort), and defined a tree as an individual with a minimum diameter of 5 cm measured at 1.3 m height (sensu Craven et al. (2018)). We included plots from each of the three main Hawaiian Islands that spanned a large precipitation gradient (Fig. 1), Hawaiʻi (ca. 0.5 Ma–200,000 years), the Maui Nui complex (ca. 2.2–1.2 Ma), which includes Maui, Molokaʻi and Lānaʻi as they formed a single landmass about 600,000 years ago, i.e., most of their geological history, and Oʻahu (ca. 3–2.6 Ma) (Price and Elliott-Fisk 2004; Clague and Sherrod 2014). Unfortunately, we were unable to include Kauaʻi, the oldest main island (ca. 5 Ma), as there were too few plots in the database available for analyses. We also excluded species of tree ferns (Cyatheales) from the analysis as they were not consistently sampled in all of the datasets (Craven et al. 2018).

We selected two versions of the forest plot dataset for our analyses. First, to evaluate the interaction between island age and the precipitation gradient, we used plots that were relatively uninvaded by alien tree species (i.e., a maximum of 40% of alien individuals), and only analyzed native tree species and species introduced by Polynesians around 800 years ago (e.g., *Cordyline fruticosa* (L.) A.Chev). We found that keeping vs. excluding the Polynesian species had no qualitative influence on the results. For these analyses, we had a total of 282 plots with 79 native species across the islands. Second, to evaluate whether including alien species in the analysis eroded the signatures of island age and/or environmental gradients, we included all available forest plots (i.e., including those with > 40% alien individuals), and considered both native and alien tree species in our analyses. For these analyses, we had a total of 375 plots with 142 species, of which 63 are alien. Species names are standardized based on The Plant List v 1.1 (Cayuela et al. 2017) in OpenNahele, and status as native or alien was obtained from the flora of the Hawaiian Islands (Wagner and Khan 2023).

Taxonomic diversity estimation at alpha scale

We computed alpha-diversity metrics for each plot using the framework of Chao and colleagues (Chao et al. 2014), which uses Hill numbers that differentially weigh common and rare species for taxonomic diversity. We used the Hill number $q = 0$, where species are weighted equally (i.e., species richness). We additionally computed the Hill number $q = 1$, which weights species equally by their abundance and $q = 2$, where abundant species are strongly influential and rare species are largely ignored. By comparing Hill numbers, which express diversity in comparable units, where taxonomic diversity quantifies the effective number of equally abundant species, we can detect if diversity patterns are driven by rare or common species (Suppl. material 1: fig. S1). This allows a meaningful and direct comparison across diversity estimates (Chao et al. 2021). The framework also controls for plots with different sample sizes; here we used sample-coverage-based rarefaction (sensu Chao et al. (2021)), which standardises to a level of sample completeness. We compared taxonomic estimates of plots using a sample completeness of 80% (i.e., sample coverage), for both analyses that included only native species and for both native and alien species. For estimating diversity, we used the taxonomic names (and abundances) of each species to calculate diversity metrics, while controlling for differences in sample effort using coverage. We calculated taxonomic diversity using the 'estimate3D' function from the iNEXT.3D package (Chao et al. 2021).

Computing species compositional turnover across the environmental gradient

To estimate the magnitude of species turnover across the precipitation gradient and evaluate whether there was an influence of island age on the magnitude of this turnover from drier to wetter sites, we used a metric of beta diversity that captures the degree to which species are non-randomly distributed across space using individual- and coverage-based rarefaction and extrapolation, called betaC (sensu Engel et al. (2021)). We used pairwise comparisons among plots for each island, comparing the betaC for a pair of plots with the absolute difference in mean annual precipitation (hereafter 'precipitation difference') among that pair. If the precipitation difference is large, plots are quite distinct in their precipitation, whereas when the difference is small, plots are in similar precipitation habitats. Because plot sizes varied considerably in this compiled dataset, we used a rarefaction approach to control for the plot size differences by randomly sampling 13 individuals (the lowest number of individuals observed in a plot) from each plot of a pair to compute betaC. We used sample completeness of 60% to compute betaC, which was the maximum possible coverage given the number of individuals (13) used in the randomization. Each randomization was repeated 100 times and we estimated the mean value of betaC for each pair of plots. Finally, tested for the effect of a different level of coverage on the betaC estimates using a lower level of sample completeness, i.e., 30%. We calculated beta diversity using the function 'betaC' from package betaC (Engel et al. 2021).

Relationship between island diversity and the environment

We compiled mean annual precipitation (MAP) and mean annual air temperature (MAT) data at the plot level using locally interpolated climate data (Giambelluca et al. 2013). To relate diversity to precipitation and temperature, we used generalized linear models with gamma family and log link, as diversity metrics are skewed and always positive. As we focus on the effect of precipitation and its variation across island age, we added an interaction term between mean annual precipitation and island. Furthermore, to account for the effect of substrate age on diversity responses (Sherrod et al. 2007), we added substrate age as a continuous variable in our models explaining alpha diversity (using the geologic map of Hawaiʻi, sensu Sherrod et al. (2007)). We then tested models in the form: Diversity ~ log(MAP) * island + substrate age + MAT, family

= Gamma(link = "log"), where diversity is taxonomic alpha diversity of the different q orders (0, 1, 2), precipitation is mean annual precipitation (mm/year), temperature is mean annual air temperature (°C) and substrate age ranges from 0 to 3 million years. We examined the contribution of temperature and substrate age explaining diversity variation using Akaike's Information Criterion (AIC), by first excluding substrate age, and then both substrate age and temperature. We further disentangled the role of substrate age within and across islands, by mapping substrate age range values and then related substrate age to both precipitation variation and diversity variation. We tested the relationship between betaC diversity and the absolute difference in mean annual precipitation using generalized linear models with gamma family and log link, with an additional interaction term between island and precipitation difference, in the form: Beta diversity ~ log(MAP difference) * island, family = Gamma(link = "log").

We determined whether the interaction between island and precipitation was significant for all models in two ways. First by plotting the model estimates and their uncertainty (85% and 95% confidence intervals), using the function 'plot_summs' in the jtools package (Long 2022), which reports the results of regression models, and thus it also tests the effect of the additional variables, i.e., mean annual air temperature and substrate age. Second, we tested the statistical significance of the interaction using the Likelihood ratio test, which compares the goodness of fit of a simpler (no interaction) versus a more complex (interaction) model. We favor the complex model with interaction if the Likelihood ratio test shows a p-value smaller than 0.05. We used the 'lrtest' function from the lmtest package (Zeileis and Hothorn 2002) to compute the Likelihood ratio test. Additionally, as the range of mean annual precipitation across islands differs, we subset precipitation to a common range for all islands (MAP > 800 & MAP < 4000) to test the consistency of the model's results for all diversity metrics. All analyses were performed in R version 4.1.0 (R Core team 2022).

Results

When we analysed patterns of alpha diversity including only relatively uninvaded plots and native species, we found a positive relationship between precipitation and taxonomic diversity on O'ahu, the oldest island in our study, but no relationship and slightly positive with precipitation on the two younger islands, Maui Nui and Hawai'i (Fig. 2A and Fig. 3A, C). This pattern was true regardless of the weighting of common versus rare species (q = 0, 1, 2) (Suppl. material 1: fig. S1). When we included plots that were highly invaded and measured alpha diversity with both native and alien species, the pattern differed (Fig. 2B). Specifically, we found a slightly stronger positive relationship between precipitation and alpha diversity for both O'ahu and Hawai'i (Fig. 2B and Fig. 3B, D). In all cases, the interaction term between island age and mean annual precipitation was significant (Suppl. material 1: table S1). Furthermore, after truncating mean annual precipitation to a common range among the three islands, we found qualitatively similar results (Suppl. material 1: fig. S2A, B), and the significant interaction between precipitation and island age on alpha diversity remained (Suppl. material 1: fig. S2C–F).

When we only considered native species in relatively less invaded plots, we found that species compositional turnover increases with precipitation differences among plots on O'ahu and Maui Nui (Fig. 2C and Fig. 3E, G). However, on Hawai'i, the compositional turnover of native species was negatively related to precipitation differences among plots (Fig. 2C and Fig. 3E, G). When we included plots that were highly invaded, we found that the relationship between species compositional turnover and precipitation differences among plots was positive for Hawai'i and O'ahu, but negative for Maui Nui (Fig. 2D and Fig. 3F, H). In all cases, the interaction term between island age and mean annual precipitation was significant (Suppl. material 1: table S1). Finally, when we redid analyses using a lower level of sample completeness (30%), we found the relationship of species compositional turnover with precipitation across islands was different, but qualitatively showed a similar pattern that turnover among different precipitation levels was higher on O'ahu (Suppl. material 1: fig. S3).

We found that the additional variables included here, temperature and substrate age, improved the explanatory power of the models (see AIC values; Suppl. material 1: table S2), where, mean annual temperature showed almost no effect on diversity and substrate age a negative effect on diversity (Fig. 3A–D). Our assessment of substrate age (Suppl. material 1: fig. S4A, B) showed that the mean geological age of an island (Fig. 1) is consistent with the local substrate age variation, that is, older islands have older substrates. Our assessment of the relation between substrate age and precipitation across islands further evidenced the lack of a clear association between the age of a substrate and precipitation amount (Suppl. material 1: fig. S4C, D). Furthermore, we found that as substrate age increased local diversity at the island level tended to decrease (Suppl. material 1: fig. S4E, F), which is consistent with the general negative effect of substrate age on diversity (Fig. 3A–D). However, our results showed that both diversity and substrate age values are always higher for the oldest island, O'ahu, than for the two younger islands.

Discussion

Older islands of the Hawaiian archipelago have more species for a given sampling effort than younger islands (Craven et al. 2019). Here, we extend these results to examine patterns across the gradient within each island–precipitation and find that the response of local diversity and species turnover to precipitation differed across islands. Specifically, the strong positive precipitation-diversity relationship on the oldest island, O'ahu (but no such strong correlation on the younger islands of Maui Nui and Hawai'i) and the

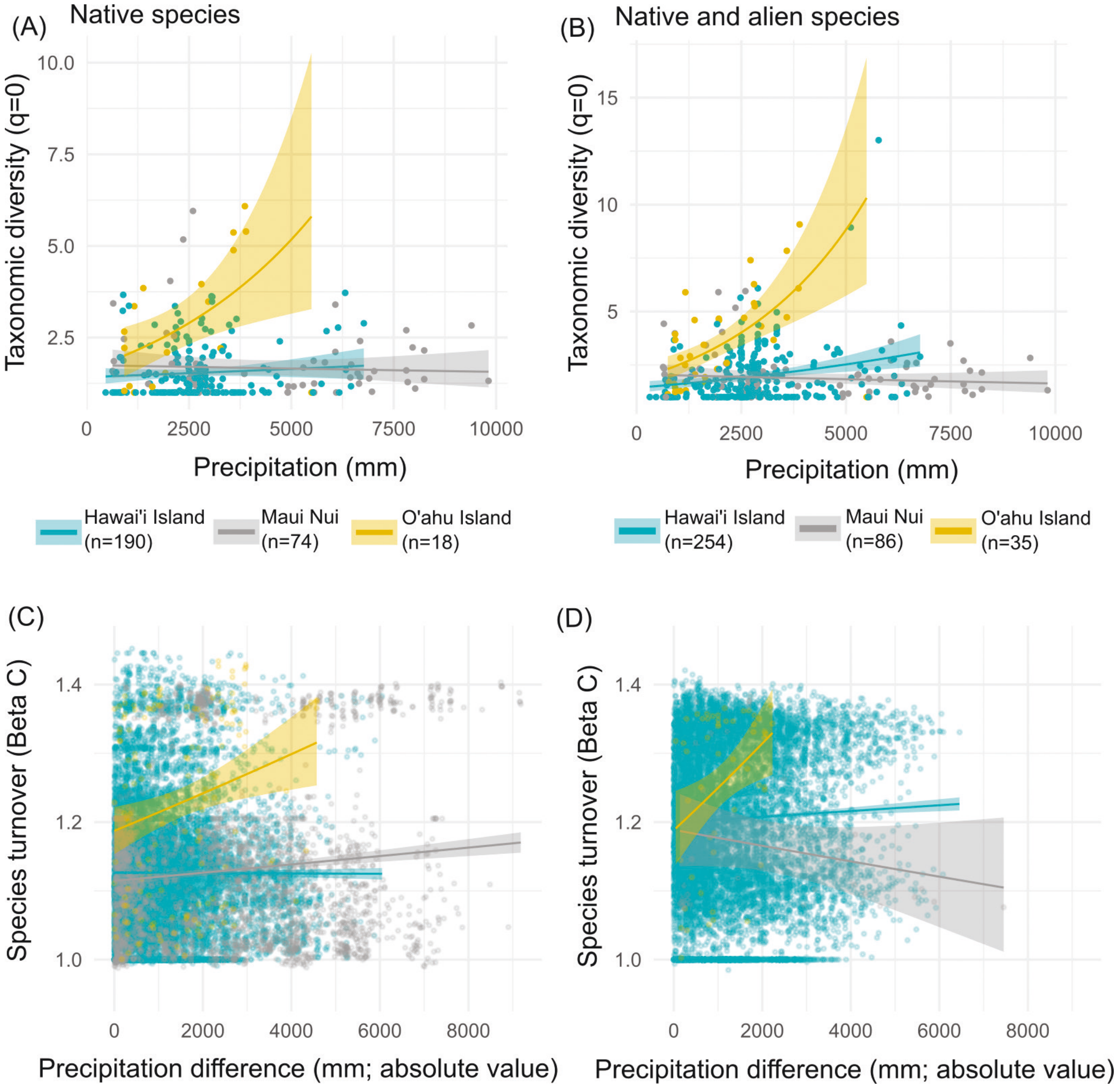

Figure 2. Response of tree diversity to mean annual precipitation for native species in relatively uninvaded plots (**A**) and both native and alien species in all plots, including those highly invaded plots (**B**), across three main Hawaiian Islands. Native species diversity includes 79 native species and is estimated from 282 plots. Native and alien species diversity estimation includes 142 species, 63 of which are alien, collected from 375 plots. Diversity metrics (a and b) are calculated based on Hill number q = 0 (i.e., species richness). Tree species turnover across the precipitation gradient in three Hawaiian Islands (c and d). Relationship between (**C**) beta diversity of native tree species in relatively uninvaded plots and mean annual precipitation difference between plot pairs and beta diversity of both native and alien tree species (**D**) (i.e., including highly invaded plots) and mean annual precipitation difference between plot pairs. Species turnover (using BetaC sensu Engel et al. (2021)) represents levels of species specialisation across dry to wet ecosystems.

increasing species turnover of native species across contrasting habitats (e.g., dry vs. wet) on O‘ahu, suggest that older islands generally provide more opportunity (time) for processes such as colonization, speciation and adaptation (Price 2004; Gillespie 2004) along with more time for ecological and successional processes (van der Sande et al. 2024) than younger islands. However, the presence of non-native species eroded these distinctions in patterns of diversity among the islands and even reversed them in the case of Maui Nui, where there was a slight negative relationship between beta diversity and precipitation distance. This suggests that local communities in different conditions became more similar to one another.

Our observed patterns of low local diversity in plots across the entire precipitation range of the island of Hawai‘i as well as the low species turnover across plots may have an alternative explanation beyond island age per se. The youngest island (Hawai‘i) has young nutrient-rich substrates, but these substrates are characterized by less developed soils. Since Hawai‘i island is in an very early stage of island ontogeny, this also results in low local soil diversity (Deenik and McClellan 2007). Undeveloped soils and low soil diversity limit opportunities for species to coexist (via niche partitioning) or create frequency-dependent feedbacks through the soil (Eppinga et al. 2018). On the island of Hawai‘i, several plots that are located in the wettest areas of

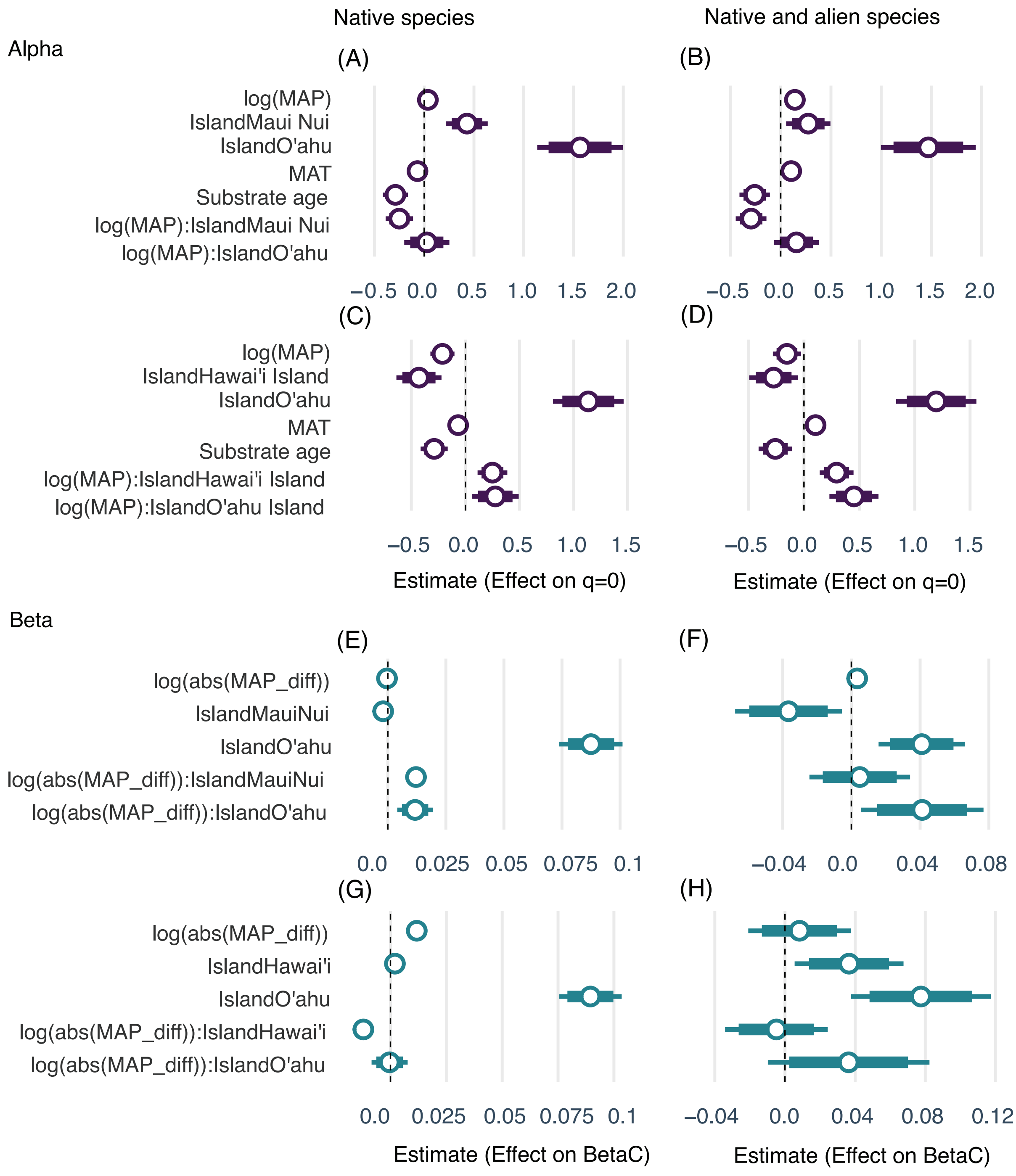

Figure 3. Assessment of the relationship of alpha and beta diversity of tree species with the environment across three main Hawaiian Islands. Models estimates showing the effect of mean annual precipitation (MAP), mean annual air temperature (MAT), and substrate age on alpha diversity of tree native species (**A**) and alpha diversity of both native and alien species (**B**). Models estimates showing the effect of precipitation difference (MAP_difference) on beta diversity of native species (**C**) and beta diversity of both native and alien species (**D**). The interaction between island age and MAP in the model assessment is shown as, for example, log(MAP):IslandO'ahu and log(abs(MAP_diff)):IslandO'ahu. Circles correspond to the value of model estimates and their uncertainties, i.e., 85% and 95% confidence intervals. Confidence intervals that do not overlap with the vertical dotted line, are considered statistically significant. Estimates comparison using Hawai'i island (i.e., '(log(MAP)' in **A**, **B**, **E**, and **F**) and Maui Nui complex island (i.e., '(log(MAP)' in **C**, **D**, **G** and **H**), as reference.

the island (> 5000 mm/year) are also located on very young substrates (0–3000 years; Suppl. material 1: fig. S4C, D) resulting from recent disruptive volcanic activity (Sherrod et al. 2007). Such conditions influence the low diversity patterns observed in highly wet areas on Hawai‘i Island. In contrast, intermediate-aged substrates, such as those found on O‘ahu, tend to have well-developed and more diverse soils (Vitousek et al. 1997; Chadwick et al. 1999) that positively affect diversity and community composition (Crews et al. 1995). Our results also show that both very high and low rainfall values occur on substrates of similar age (particularly on Hawaiʻi Island; Suppl. material 1: fig. S4C, D), therefore rainfall values vary greatly along substrate age. However, the range of substrate age across islands (Suppl. material 1: fig. S4A, B) indicates that substrate age is highly dependent on the island's overall average age. This is due to the geological characteristics of the Hawaiian hotspot, which forms a linear chain of islands with more active eruptions on the younger islands (Sherrod et al. 2007), thus, older Hawaiian Islands tend to have older substrates.

Although temperature is a main driver of plant diversity, the lack of a significant effect of annual temperature on species diversity at the island level suggests that both warm and relatively cold areas can exhibit similar diversity values. However, the rather limited temperature range (8–23 °C) covered in our study, may influence these results. Additionally, further environmental conditions and dynamics, which we did not directly test here, can influence the patterns of tree diversity observed. Water-energy dynamics shape tree diversity, e.g., influencing tree growth. In wet environments, such dynamics play a role by providing trees with high water, energy, and nutrient availability (Field et al. 2005; O'Brien 2006), which can positively affect diversity in the wet environments studies here. Differences in island topographic complexity also modulate the diversity. Topographically complex islands such as Oʻahu, tend to have high levels of environmental heterogeneity and habitat diversity, which also positively influence diversity (Barajas-Barbosa et al. 2020).

Our result of a positive relationship between native species turnover and the precipitation difference among plots on Oʻahu and Maui Nui, but not Hawaiʻi, reinforces the idea that there has been more time for eco-evolutionary assembly of species that specialize in different environments and habitat types, as well as for new specialised colonists to establish in those habitats. This may relate to a high niche differentiation occurring on older islands; whereby diversity is promoted in wet environments, potentially due to the more favorable abiotic conditions than in dry environments (Spasojevic et al. 2014). This result is also consistent with the idea that macroevolutionary time provides more opportunities for species adaptation and specialisation into different habitat types; yet, the high heterogeneity in soil types and topography of older islands may also allow more species to coexist in the wetter environments (Mason et al. 2012; Laliberté et al. 2013). Species generally have a limited ability to adapt to dry environments (Ringelberg et al. 2023) and, therefore, they tend to retain ecological preferences through evolutionary time via niche conservatism (Barajas-Barbosa et al. 2023). Therefore, adaptation and colonisation of species in dry areas of the older island may also be limited. This likely influenced the lower diversity we observed in Oʻahu's arid environments. Furthermore, the low species turnover observed on the youngest island, Hawaiʻi, can be explained by the presence of several native species in plots across wet and dry habitats such as *Metrosideros polymorpha* Gaudich (Myrtaceae), *Cheirodendron trigynum* A.Heller (Araliaceae) and *Ilex anomala* Hook. & Arn. (Aquifoliaceae). These species exhibit great versatility to occur in contrasting habitats, from very recent lava flows to substrates that are millions of years old. While these species prefer moist habitats, they can tolerate a large range of annual precipitation levels (Barton et al. 2021). This, together with the possible lower competition on younger islands due to lower species diversity (Borregaard et al. 2016; Craven et al. 2019), may allow such generalist species to be more successful across the steep precipitation gradient and contribute to the low diversity specialization pattern observed on the young island.

While we hypothesised that the biodiversity patterns might weaken when we included heavily invaded plots (e.g., through homogenisation), we actually found distinctly new patterns rather than a weakening of existing patterns (Fig. 2B, D). For example, we found no trends in diversity or species turnover with precipitation on the youngest island of Hawaiʻi when only plots dominated by native species were examined, but these relationships became positive when we included the highly invaded plots. This may be for two reasons. First, several of the invaded plots that were in wet areas contained relatively high native tree diversity (in terms of species number) and thus contributed to the trend for increasing tree diversity with increasing precipitation. These plots in wet areas were often invaded by *Psidium cattleianum* Afzel. ex Sabine, a highly abundant invasive tree that may eventually displace these native trees but has not yet done so (Barton et al. 2021). Second, many of the invasive species have preferences for different precipitation conditions. For example, the invaders *Leucaena leucocephala* (Lam.) de Wit, *Pinus spps* and *Schinus terebinthifolia* Raddi tend to occur more in drier plots, while *Psidium cattleianum* and *Myrica faya* (Dryand.) Aiton occur more in wet plots, creating turnover between wetter and drier plots. In contrast, on Maui Nui island complex, there was a decrease in beta diversity with increasing precipitation difference when we included heavily invaded plots (Fig. 2D). That is, local diversity of both native and alien species on Maui Nui was higher in more arid than in wet environments when we included heavily invaded plots and alien species. This could be because Maui Nui was uniquely invaded by arid-favouring species or because alien species have a greater establishment and impact on native species diversity in wetter environments. While we cannot definitively test these hypotheses, the former would not explain why species turnover across plots declines as precipitation amount becomes more different on Maui Nui, as the opposite pattern would be expected. It is therefore likely that alien species are negatively affecting the native species in the wetter parts of Maui Nui.

Lastly, the imprint of geological time on local diversity (alpha) and species turnover (beta) diversity patterns of oceanic archipelagos can be weakened by the effect of dispersal. Particularly for the Hawaiian archipelago, where 89% of the flowering plants are endemic (Wagner and Khan 2023), inter-island dispersal may confound the effect of time, as lineages that evolved or adapted in environments of older islands can colonize younger ones. Despite this, the patterns observed here in older and younger Hawaiian Islands reinforce the fact that time not only promotes overall diversity but may also influence the ability of species to specialize in distinct environmental conditions.

Conclusions

Overall, we found that the response of Hawaiian native tree diversity to precipitation varies across different islands on the archipelago. Specifically, we found that in the absence of alien species tree diversity strongly responded to gradients of precipitation on the older island, affecting both local diversity and the turnover of species across habitats with different levels of precipitation. These patterns were not evident on the younger islands. This suggests that geological time, by moderating the ecological and macroevolutionary processes of communities, might play a role in determining how patterns of diversity respond to the environment. Other factors that vary greatly across the islands, such as soil diversity and water-energy dynamics, which were not tested here, may also play a critical role in shaping tree diversity. Finally, we find that the introduction of alien species modifies the precipitation-diversity relationship of native island floras and obscures the pattern of native species across islands. This indicates that the ongoing invasion of the Hawaiian Islands will fundamentally reshape the local biodiversity patterns of trees and the ecosystem services this biodiversity offers.

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Author contributions statement

M. Paola Barajas Barbosa performed study conceptualization, data preparation, analysis, and writing. Tiffany M. Knight performed study conceptualization and writing. Renske Onstein performed analysis and writing. Jonathan Chase performed study conceptualization and writing.

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Code and data accessibility statement

Data and code related to the analysis of this paper is available at: https://doi.org/10.6084/m9.figshare.27933666.v1 and https://github.com/paolabarajas/Diversity-respons-es-in-Hawaii-precipitation-.

Conflict of interest statement

The authors declare no competing financial interests.

References

Adler PB, Levine JM (2007) Contrasting relationships between precipitation and species richness in space and time. Oikos 116: 221–232. https://doi.org/10.1111/j.0030-1299.2007.15327.x

Baldwin BG (1997) Adaptive radiation of the Hawaiian silversword alliance: congruence and conflict of phylogenetic evidence from molecular and non-molecular investigations. Molecular Evolution and Adaptive Radiation 103: 1840–1843.

Barajas-Barbosa MP, Weigelt P, Borregaard MK, Keppel G, Kreft H (2020) Environmental heterogeneity dynamics drive plant diversity on oceanic islands. Journal of Biogeography 47: 2248–2260. https://doi.org/10.1111/jbi.13925

Barajas Barbosa MP, Craven D, Weigelt P, Denelle P, Otto R, Díaz S, Price J, Fernández-Palacios JM, Kreft H (2023) Assembly of functional diversity in an oceanic island flora. Nature 619: 545–550. https://doi.org/10.1038/s41586-023-06305-z

Barton KE, Westerband A, Ostertag R, Stacy E, Winter K, Drake DR, Fortini LB, Litton CM, Cordell S, Krushelnycky P, Kawelo K, Feliciano K, Bennett G, Knight T (2021) Hawaiʻi forest review: synthesizing the ecology, evolution, and conservation of a model system. Perspectives in Plant Ecology, Evolution and Systematics 52: 125631. https://doi.org/10.1016/j.ppees.2021.125631

Borregaard MK, Matthews TJ, Whittaker RJ (2016) The general dynamic model: towards a unified theory of island biogeography? Global Ecology and Biogeography 25: 805–816. https://doi.org/10.1111/geb.12348

Brown RF, Siler CD, Oliveros CH, Esselstyn J, Diesmos A, Hosner P, Linkem C, Barley A, Oaks J, Sanguila M, Welton L, Blackburn D, Moyle R, Peterson A, Alcala A (2013) Evolutionary processes of diversification in a model island archipelago. Annual Review of Ecology, Evolution, and Systematics 44: 411–435. https://doi.org/10.1146/annurev-ecolsys-110411-160323

Cayuela L, Macarro I, Stein A, Oksanen J (2017) Package ‘Taxonstand’. https://cran.irsn.fr/web/packages/Taxonstand/Taxonstand.pdf

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397: 491–497. https://doi.org/10.1038/17276

Chao A, Chiu C-H, Jost L (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. Annual Review of Ecology, Evolution, and Systematics 45: 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chao A, Henderson PA, Chiu C, Moyes F, Hu K, Dornelas M, Magurran AE (2021) Measuring temporal change in alpha diversity: a framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. Methods in Ecology and Evolution 12: 1926–1940. https://doi.org/10.1111/2041-210X.13682

Clague DA (1996) The growth and subsidence of the Hawaiian-Emperor volcanic chain. In: The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes. US Geological Survey Report, 35–50.

Clague DA, Sherrod DR (2014) Growth and degradation of Hawaiian volcanoes: In: Characteristics of Hawaiian volcanoes. Geological Survey Professional Paper 1801. https://pubs.usgs.gov/pp/1801/downloads/pp1801_Chap3_Clague.pdf

Craven D, Knight T, Barton K, Bialic-Murphy L, Cordell S, Giardina C, Gillespie T, Ostertag R, Sack L, Chase J (2018) OpenNahele: the open Hawaiian forest plot database. Biodiversity Data Journal 6: e28406. https://doi.org/10.3897/BDJ.6.e28406

Craven D, Knight TM, Barton KE, Bialic-Murphy L, Chase JM (2019) Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. Proceedings of the National Academy of Sciences USA 116: 16436–16441. https://doi.org/10.1073/pnas.1901954116

Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. Ecology 76: 1407–1424. https://doi.org/10.2307/1938144

Deenik J, McClellan AT (2007) Soils of Hawaii. College of Tropical Agriculture and Human Resources (CTAHR), University of Hawaiʻi at Mänoa, and U.S. Department of Agriculture, Hawaiʻi. https://www.ctahr.hawaii.edu/oc/freepubs/pdf/scm-20.pdf

Díaz S, Malhi Y (2022) Biodiversity: concepts, patterns, trends, and perspectives. Annual Review of Environment and Resources 47: 31–63. https://doi.org/10.1146/annurev-environ-120120-054300

Engel T, Blowes SA, McGlinn DJ, May F, Gotelli NJ, McGill BJ, Chase JM (2021) Using coverage-based rarefaction to infer non-random species distributions. Ecosphere 12: e03745. https://doi.org/10.1002/ecs2.3745

Eppinga MB, Baudena M, Johnson DJ, Jiang J, Mack KML, Strand AE, Bever JD (2018) Frequency-dependent feedback constrains plant community coexistence. Nature Ecology & Evolution 2: 1403–1407. https://doi.org/10.1038/s41559-018-0622-3

Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, ter Steege H, Lopez-Gonzalez G, Monteagudo Mendoza A, Brienen R, Feldpausch TR, Pitman N, Alonso A, van der Heijden G, Peña-Claros M, Ahuite M, Alexiaides M, Álvarez Dávila E, Araujo Murakami A, Arroyo L, Aulestia M, Balslev H, Barroso J, Boot R, Cano A, Chama Moscoso V, Comiskey JA, Cornejo F, Dallmeier F, Daly DC, Dávila N, Duivenvoorden JF, Duque Montoya AJ, Erwin T, Di Fiore A, Fredericksen T, Fuentes A, García-Villacorta R, Gonzales T, Guevara Andino JE, Honorio Coronado EN, Huamantupa-Chuquimaco I, Jiménez REM, Killeen TJ, Malhi Y, Mendoza C, Mogollón H, Møller Jørgensen P, Montero JC, Mostacedo B, Nauray W, Neill D, Núñez Vargas P, Palacios S, Palacios Cuenca W, Pallqui Camacho NC, Peacock J, Phillips JF, Pickavance G, Quesada CA, Ramírez-Angulo H, Restrepo Z, Reynel Rodriguez C, Ríos Paredes M, Peñuela-Mora MC, Sierra R, Silveira M, Stevenson P, Stropp J, Terborgh J, Tirado M, Toledo M, Torres-Lezama A, Umaña MN, Urrego LE, Vasquez Martinez R, Valenzuela Gamarra L, Vela CIA, Vilanova Torre E, Vos V, von Hildebrand P, Vriesendorp C, Wang O, Young KR, Zartman CE, Phillips OL (2017) Seasonal drought limits tree species across the Neotropics. Ecography 40: 618–629. https://doi.org/10.1111/ecog.01904

Field R, O'Brien EM, Whittaker RJ (2005) Global models for predicting woody plant richness from climate: development and evaluation. Ecology 86: 2263–2277. https://doi.org/10.1890/04-1910

Giambelluca TW, Chen Q, Frazier AG, Price JP, Chen Y-L, Chu P-S, Eischeid JK, Delparte DM (2013) Online rainfall atlas of Hawaiʻi. Bulletin of the American Meteorological Society 94: 313–316. https://doi.org/10.1175/BAMS-D-11-00228.1

Gillespie RG (2001) Oceanic islands: models of diversity. In: Encyclopedia of Biodiversity, 590–599, Elsevier. https://doi.org/10.1016/B978-0-12-384719-5.00231-8

Gillespie RG (2004) Community assembly through adaptive radiation in Hawaiian spiders. Science 303: 356–359. https://doi.org/10.1126/science.1091875

Gillespie RG, Baldwin BG (2010) Island biogeography of remote archipelagos. The Theory of Island Biogeography Revisited: 358–387. https://doi.org/10.1515/9781400831920.358

Gillespie RG (2016) Island time and the interplay between ecology and evolution in species diversification. Evolutionary Applications 9: 53–73. https://doi.org/10.1111/eva.12302

Givnish TJ (1999) On the causes of gradients in tropical tree diversity. Journal of Ecology 87: 193–210. https://doi.org/10.1046/j.1365-2745.1999.00333.x

Givnish TJ, Millam KC, Mast AR, Paterson TB, Theim TJ, Hipp AL, Henss JM, Smith JF, Wood KR, Sytsma KJ (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). Proceedings of the Royal Society B: Biological Sciences 276: 407–416. https://doi.org/10.1098/rspb.2008.1204

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. The American Naturalist 163: 192–211. https://doi.org/10.1086/381004

Idárraga-Piedrahíta Á, González-Caro S, Duque ÁJ, Jiménez-Montoya J, González-M R, Parra JL, Rivera-Gutiérrez HF (2022) Drivers of beta diversity along a precipitation gradient in tropical forests of the Cauca River Canyon in Colombia. Journal of Vegetation Science 33: e13110. https://doi.org/10.1111/jvs.13110

Keil P, Chase JM (2019) Global patterns and drivers of tree diversity integrated across a continuum of spatial grains. Nature Ecology and Evolution 3: 390–399. https://doi.org/10.1038/s41559-019-0799-0

Korell L, Auge H, Chase JM, Harpole WS, Knight TM (2021) Responses of plant diversity to precipitation change are strongest at local spatial scales and in drylands. Nature Communications 12: 2489. https://doi.org/10.1038/s41467-021-22766-0

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences USA 104(14): 5925–5930. https://doi.org/10.1073/pnas.0608361104

Laliberté E, Grace JB, Huston MA, Lambers H, Teste FP, Turner BL, Wardle DA (2013) How does pedogenesis drive plant diversity? Trends in Ecology & Evolution 28: 331–340. https://doi.org/10.1016/j.tree.2013.02.008

Lim JY, Marshall CR (2017) The true tempo of evolutionary radiation and decline revealed on the Hawaiian archipelago. Nature 543: 710–713. https://doi.org/10.1038/nature21675

Long JA (2022) jtools: analysis and presentation of social scientific data. R package version 2.2.0. https://cran.r-project.org/web/packages/jtools/index.html

Magurran AE (2021) Measuring biological diversity. Current Biology 31: R1174–R1177. https://doi.org/10.1016/j.cub.2021.07.049

Mason NWH, Richardson SJ, Peltzer DA, de Bello F, Wardle DA, Allen RB (2012) Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. Journal of Ecology 100: 678–689. https://doi.org/10.1111/j.1365-2745.2012.01965.x

Nogué S, Santos AMC, Birks HJB, Björck S, Castilla-Beltrán A, Connor S, de Boer EJ, de Nascimento L, Felde V, Fernández-Palacios JM, Froyd C, Haberle S, Hooghiemstra H, Ljung K, Norder S, Peñuelas J, Prebble M, Stevenson J, Whittaker RJ, Willis K, Wilmshurst J, Steinbauer MJ (2021) The human dimension of biodiversity changes on islands. Science 372: 488–491. https://doi.org/10.1126/science.abd6706

O’Brien EM (2006) Biological relativity to water–energy dynamics. Journal of Biogeography 33: 1868–1888. https://doi.org/10.1111/j.1365-2699.2006.01534.x

Price JP (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. Journal of Biogeography 31: 487–500. https://doi.org/10.1046/j.0305-0270.2003.00990.x

Price JP, Elliott-Fisk D (2004) Topographic history of the Maui Nui complex, Hawai‘i, and its implications for biogeography. Pacific Science 58: 27–45. https://doi.org/10.1353/psc.2004.0008

R Core team (2022) R: a language and environment for statistical computing. Vienna, Austria. [Retrieved 01/09/2024, from] https://www.R-project.org/

Ringelberg JJ, Koenen EJM, Sauter B, Aebli A, Rando JG, Iganci JR, de Queiroz LP, Murphy DJ, Gaudeul M, Bruneau A, Luckow M, Lewis GP, Miller JT, Simon MF, Jordão LSB, Morales M, Bailey CD, Nageswara-Rao M, Nicholls JA, Loiseau O, Pennington RT, Dexter KG, Zimmermann NE, Hughes CE (2023) Precipitation is the main axis of tropical plant phylogenetic turnover across space and time. Science Advances 9: eade4954. https://doi.org/10.1126/sciadv.ade4954

Russell JC, Kueffer C (2019) Island biodiversity in the Anthropocene. Annual Review of Environment and Resources 44: 31–60. https://doi.org/10.1146/annurev-environ-101718-033245

van der Sande MT, Poorter L, Derroire G, do Espirito Santo M, Lohbeck M, Müller SC, Bhaskar R, van Breugel M, Dupuy-Rada JM, Durán SM, Jakovac CC, Paz H, Rozendaal DMA, Brancalion P, Craven D, Mora Ardilla F, Almeida JS, Balvanera P, Becknell J, Finegan B, Gomes César R, Hernández-Stefanoni JL, Kennard D, Letcher SG, Marín-Spiotta E, Muñoz R, Reyes-García C, Sanaphre-Villanueva L, Utrera LP, Fernandes GW, Álvarez FS, Andrade JL, Arreola F, Boukili V, Cabral GAL, Chave J, Chazdon R, Colletta G, Magalhães Veloso MdD, de Jong B, Lebrija-Trejos E, de Souza Moreno V, Dent DH, DeWalt S, Díaz García E, Ferreira Nunes YR, Granda V, Hall J, Lobo R, Lopez O, Martínez Ramos M, Meave JA, Ochoa-Gaona S, Sampaio EVSBS, Sanchez-Azofeifa A, Teixeira HM, Toledo M, Uriarte M, Wright SJ, Zanini K, Bongers F (2024) Tropical forest succession increases tree taxonomic and functional richness but decreases evenness. Global Ecology and Biogeography 33: e13856. https://doi.org/10.1111/geb.13856

Sandel B, Weigelt P, Kreft H, Keppel G, van der Sande MT, Levin S, Smith S, Craven D, Knight TM (2020) Current climate, isolation and history drive global patterns of tree phylogenetic endemism. Global Ecology and Biogeography 29: 4–15. https://doi.org/10.1111/geb.13001

Segovia RA, Pennington RT, Baker TR, Coelho de Souza F, Neves DM, Davis CC, Armesto JJ, Olivera-Filho AT, Dexter KG (2020) Freezing and water availability structure the evolutionary diversity of trees across the Americas. Science Advances 6: eaaz5373. https://doi.org/10.1126/sciadv.aaz5373

Shaw KL, Gillespie RG (2016) Comparative phylogeography of oceanic archipelagos: hotspots for inferences of evolutionary process. Proceedings of the National Academy of Sciences USA 113: 7986–7993. https://doi.org/10.1073/pnas.1601078113

Sherrod DR, Sinton JM, Watkins SE, Brunt KM (2007) Geologic map of the State of Hawai‘i. US Geological Survey Open-File Report 1089: 83. https://doi.org/10.3133/ofr20071089

Spasojevic MJ, Grace JB, Harrison S, Damschen EI (2014) Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. Journal of Ecology 102: 447–455. https://doi.org/10.1111/1365-2745.12204

Vitousek PM, Chadwick OA, Crews TE, Fownes JH, Hendricks DM, Herbert D (1997) Soil and ecosystem development across the Hawaiian Islands. GSA Today 7: 1–8.

Wagner WL, Khan NR (2023) Flora of the Hawaiian Islands website. https://naturalhistory2.si.edu/botany/hawaiianflora/ [May 2023]

Warren BH, Simberloff D, Ricklefs RE, Aguilée R, Condamine F, Gravel D, Morlon H, Mouquet N, Rosindell J, Casquet J, Conti E, Cornuault J, Fernández-Palacios JM, Hengl T, Norder S, Rijsdijk KF, Sanmartín I, Strasberg D, Triantis K, Valente L, Whittaker RJ, Gillespie RG, Emerson B, Thébaud C (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. Ecology Letters 18: 200–217. https://doi.org/10.1111/ele.12398

Whittaker RJ, Heegaard E (2003) What is the observed relationship between species richness and productivity? Comment. Ecology 84: 3384–3390. https://doi.org/10.1890/02-3128

Whittaker RJ, Triantis KA, Ladle RJ (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography 35: 977–994. https://doi.org/10.1111/j.1365-2699.2008.01892.x

Whittaker RJ, Fernández-Palacios JM, Matthews TJ, Borregaard MK, Triantis KA (2017) Island biogeography: taking the long view of nature’s laboratories. Science 357: eaam8326. https://doi.org/10.1126/science.aam8326

Wilson EO (1988) Biodiversity. National Academies Press. Harvard University. Washington D.C.

Zeileis A, Hothorn T (2002) Diagnostic checking in regression relationships. https://journal.r-project.org/articles/RN-2002-018/RN-2002-018.pdf

Supplementary materials

Supplementary material 1

figure S1. Relationship between mean annual precipitation and alpha diversity; figure S2. Relationship for mean annual precipitation truncated to common precipitation among islands; figure S3. Sensitivity analysis on the effect of the different coverage on the betaC metrics; figure S4. Assessment of substrate age in relation to mean annual precipitation and diversity across plots and islands; table S1. Statistical significance of the interaction term between island and mean annual precipitation; table S2. Evaluation of models including mean annual temperature and substrate age. (.docx)
Link: https://doi.org/10.21425/fob.18.131129.suppl1