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Research Article

Slowing taxon cycle can explain biodiversity patterns on islands: Insights into the biogeography of the tropical South Pacific from molecular data

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Abstract Islands in the tropical Pacific Ocean are renowned for high biodiversity and endemism despite having relatively small landmasses. However, our knowledge of how this biodiversity is formed remains limited. The taxon cycle, where well-dispersed, earlier colonizers become displaced from coastal to inland habitats by new waves of colonizers, producing isolated, range-restricted species, has been proposed to explain current biodiversity patterns. Here, we integrate the outcomes of phylogenetic studies in the region to investigate the sources, age, number of colonizations, and diversification of 16 archipelagos in the tropical and subtropical South Pacific. We then evaluate whether the results support the taxon cycle as a plausible mechanism for these observations. We find that most species in the Pacific arrived less than 5 Mya from geographically close sources, suggesting that colonization by new taxa is a frequent and ongoing process. Therefore, our findings are broadly consistent with the theory of the Taxon Cycle, which posits that ongoing colonization results in the gradual displacement of established lineages. Only the oldest archipelagos, New Caledonia and Fiji, do not conform to this trend, having proportionally less recent colonization events, suggesting that the taxon cycle may slow on older islands. This conclusion is further validated by New Caledonia having lower diversification rate estimates than younger islands. We found that diversification rates across archipelagos are negatively correlated with area and age. Therefore, a taxon cycle that slows with island age appears to be a suitable concept for understanding the dynamic nature and biodiversity patterns of the Pacific Islands.

Key words: colonization, diversification, island biogeography, Pacific, phylogeography, taxon cycle.

1 Introduction

The insular tropical Pacific (Fig. 1) is rich in biodiversity and endemism (Kier et al., 2009; Ibanez et al., 2017). For example, it is home to about 2% of the world's orchid diversity on less than 0.1% of our planet's terrestrial surface, with more than 50% of the species being endemic to the region (Keppel et al., 2016). This abundant and unique biodiversity is also highly threatened and vulnerable, and most islands are part of one of the world's 36 global biodiversity hotspots (Mittermeier et al., 2011; Keppel et al., 2014). However, biodiversity is not equally distributed, as older, larger islands with greater environmental heterogeneity are more diverse (MacArthur & Wilson, 1967; Keppel et al., 2009, 2016).

Despite its importance, the tropical Pacific remains understudied (Smith & Brown, 2018; Keppel et al., 2021; Cerca et al., 2023). Furthermore, the biodiversity of independent island nations has been little studied compared to territories administered by nations outside the insular Pacific (Keppel et al., 2012; Brodie et al., 2013). This is exemplified by studies using aggregated molecular studies being restricted to the predominantly externally controlled regions of the Galapagos (Parent et al., 2008; García-Verdugo et al., 2014), Hawaii (Price & Wagner, 2018), Marquesas (Hembry, 2018), Micronesia (Demeulenaere & Ickert-Bond, 2022), and New Caledonia (Pillon, 2012; Nattier et al., 2017). A holistic picture of the history and evolution of biodiversity in the tropical Pacific is therefore lacking.

Studies in the tropical Pacific have contributed to numerous important biological discoveries, including the theory of evolution (Darwin, 1859), the theory of island biogeography (MacArthur & Wilson, 1963, 1967), and the taxon cycle (Wilson, 1959, 1961). The theory of the taxon cycle posits that islands are mostly colonized by widespread,

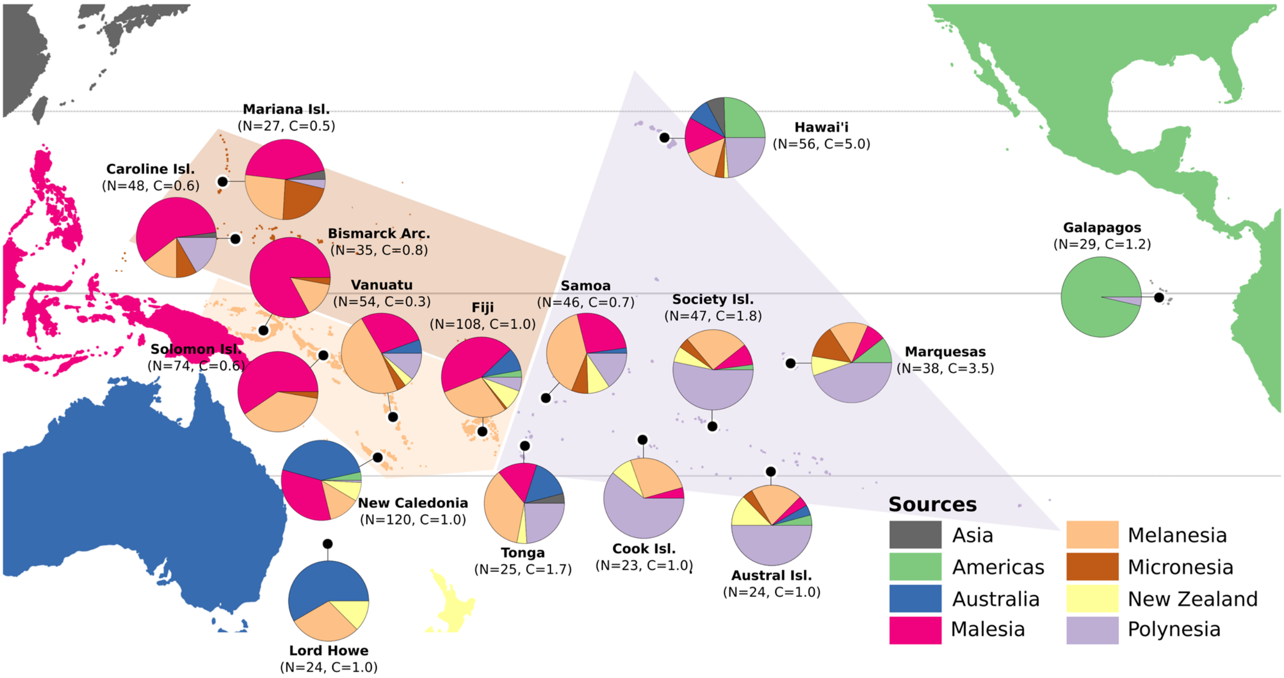

Fig. 1. The tropical and subtropical South Pacific and the sources and colonization ratios for 16 focal archipelagos. The pie charts indicate the proportion of colonization events originating in the various color-coded source areas. C, colonization ratio (the ratio of lineages originating from a single colonization event to those originating from multiple colonization events); *N*, number of colonization events.

well-dispersed taxa of ecological generalists, which diversify and are eventually displaced to inland habitats by new waves of colonizers to produce fragmented lineages of multiple species that are derived from the earlier colonizers (Wilson, 1961; Pepke et al., 2019). During the first stage of the cycle, a taxon expands its geographic range by dispersing into coastal areas of islands over a wide geographic range (Wilson, 1961; Pepke et al., 2019) and such taxa have been referred to as "supertramps" (Diamond, 1974). Subsequently, the taxon expands to habitats further inland and populations on different islands may differentiate, possibly due to reduced dispersal capabilities (Wilson, 1961; Pepke et al., 2019). Taxa at this stage are sometimes referred to as "great speciators" (Diamond et al., 1976).

At stage three, diversification of populations has resulted in speciation, which can include adaptive radiation to fill available niches (Goodman et al., 2014). While the taxon attains its highest diversity at this stage, it also begins to contract due to displacement in coastal habitats by new colonizers (Wilson, 1961; Pepke et al., 2019). The increasing isolation of populations, due to inland habitats being less connected than coastal ones, likely reinforces speciation. The contraction of the taxon continues, unless a new wave of expansion is initiated (Matos-Maraví et al., 2018), increasing the likelihood of extinction and producing relictual taxa on larger islands with greater elevation at this final stage. Recent phylogenies of Pacific taxa tend to support the expectations of the taxon cycle (Matos-Maraví et al., 2018; Oliver et al., 2018; Pedersen et al., 2018; Pepke et al., 2019).

Unlike the theory of island biogeography, which suggests that the species diversity of an island is maintained by an equilibrium of immigration and extinction (MacArthur & Wilson, 1967) and is most readily applicable to islands within an archipelago (Whittaker et al., 2008; Carey et al., 2020, 2023), the expectations of the taxon cycle are best tested across archipelagos. The tropical South Pacific provides a suitable study area to investigate the taxon cycle hypothesis because both geological (Hall, 2002; Neall & Trewick, 2008) and molecular (Keppel et al., 2009; Nattier et al., 2017) data suggest that (almost) all biota can be considered to have originated via transoceanic dispersal and islands are of different ages, isolation, area, and environmental heterogeneity. Even the continental fragment of New Caledonia was likely completely submerged before re-emergence some 33 Mya (Cluzel et al., 2012; Pillon, 2012; Nattier et al., 2017), suggesting that the region's biodiversity was assembled less than 40 Mya.

Here we use published molecular studies across 16 archipelagos to better understand the evolution of the biota in the tropical South Pacific. In particular, we sought to answer the following questions for each lineage in these archipelagos: (i) where did colonizers originate? (ii) when did they arrive? and (iii) did they colonize an archipelago once or multiple times? We then investigate the relative importance of archipelago age, area, and isolation in the evolution of the biota and relate our predictions to the expectations underlying the taxon cycle hypothesis. Regarding source areas, we expected that most colonization events originated from sources in closer proximity, as the taxon cycle predicts initial colonizers to be widespread ecological generalists. Furthermore, the taxon cycle would suggest that most of the biota in an archipelago is of recent origin, as displacement (and, potentially, eventual extinction) of earlier colonizers occurs. Finally, one would expect that overall (across all taxa) diversification rates on younger archipelagos are higher because many taxa that resulted from earlier colonization events on older archipelagos would have become extinct.

2 Material and Methods

2.1 Data collection and preparation

We identified relevant literature by searching the *Web of Science* using the keywords "Pacific AND island* AND phylo*." Results were supplemented with references in synthesis studies that reviewed phylogenetic relationships in the tropical South Pacific (Keppel et al., 2009) or in particular archipelagos within this region: Galapagos (Parent et al., 2008; García-Verdugo et al., 2014), Hawaii (Price & Wagner, 2018), Marquesas (Hembry, 2018), Micronesia (Demeulenaere & Ickert-Bond, 2022), and New Caledonia (Pillon, 2012; Nattier et al., 2017). We excluded studies for which sampling did not cover large portions of a taxon's distribution, such as studies with detailed sampling in only one or two archipelagos for taxa found in many Pacific archipelagoes. For example, the work on orb-weaver spiders of the genus *Tetragnatha* in Hawaii, the Marquesas, and the Society Islands (Gillespie, 2002) was excluded because the genus occurs throughout Polynesia and Melanesia, and most archipelagos were not sampled. This resulted in 156 publications being analyzed (Table S1).

We recorded data for every colonization event that could be inferred, meaning that a taxon reported as polyphyletic for an archipelago would have multiple colonization events. For example, for the genus *Cyrtandra* (Gesneriaceae) four colonization events were inferred for both the Samoa and Vanuatu archipelagos based on the data provided (Johnson et al., 2017). We used the consensus tree of sequences if multiple trees were provided. For each colonization event, we recorded: the name of the taxon (with family and phylum affiliation), the name of the target archipelago, the inferred source of the colonization event, the source of lineage, the stem and crown age of the group (where available), the number of taxa included in the study, whether the radiation was monophyletic, the loci used, and the reference source for the data. Furthermore, we derived the estimated age and colonization ratio for each archipelago. Each variable is described in Table 1 with its limitations. We only retained archipelagos for which at least 20 colonization events were available. All analyses were undertaken in the R statistical environment (R Core Team, 2023).

2.2 Diversification rates

To be included in our diversification analyses, a clade needed to fulfill three criteria: (i) be monophyletic, that is, exclusion of lineages that colonized an archipelago repeatedly because the total number of endemic species per clade could not be fully determined unless the clades were 100% sampled, (ii) consist of ≥3 species, which is the threshold previously implemented for radiations (see Cerca et al., 2023) and, (iii) be part of an archipelago with seven or more included clades available to ensure adequate number of datapoints for statistical analyses. This produced a filtered data set for diversification that included eight archipelagos.

We applied the method of moments approach (Magallon & Sanderson, 2001) to obtain estimates of diversification rates from phylogenetic metadata (stem/crown age), allowing us to incorporate a greater number of datapoints to account for the limited phylogenetic sampling present across most Pacific archipelagos. Indeed, as many of the clades present across the Pacific are small in size (<10 species), inferring diversification rates from methods that rely on larger data sets would be challenging (Cusimano & Renner, 2010). While the method of moments approach has been criticized for its nonidentifiability (Rabosky & Benson, 2021), this limitation is not specific to this approach but rather pertains to all diversification models (Louca & Pennell, 2020). Furthermore, simulation studies have shown this method to be a valid and reliable approach for estimating diversification (Kozak & Wiens, 2016; Román-Palacios & Wiens, 2018). Diversification rates were calculated from both stem and crown ages, respectively, for stem: $\hat{r}_\varepsilon = \frac{1}{t}\log[n(1-\varepsilon)+\varepsilon]$, and crown:

$$\hat{r}_\in = \frac{1}{t}\left\{\log\left[\frac{1}{2}n(1-\in^2)+2\in+\frac{1}{2}(1-\in)\sqrt{n(n\in^2-8\in+2n\in+n)}\right]-\log 2\right\},$$

where r represents the net diversification rate, n represents diversity, t represents age, and ε represents the relative extinction fraction (e.g., an ε value of 0.9 corresponds to clades that have less than 10% of extant lineages surviving to the present). The diversification rate of each lineage was calculated using the *geiger* v2.0.7 package (Harmon et al., 2007) using two input variables: (i) the stem or crown age of each endemic clade per region and (ii) the number of extant species for each endemic lineage per region. We calculated diversification rates with two relative extinction fractions: $\varepsilon = 0$ (pure birth) and $\varepsilon = 0.9$ (high relative extinction). As we have fewer datapoints for crown age estimates (across only four archipelagos), we focused on diversification rates derived from stem ages.

2.3 Rationale for method of moments

The calculation of diversification rates based on stem age and species in a clade is dependent on the sampling of respective clades. In most cases, the sampling was incomplete (i.e., published phylogenies did not include all species found on an archipelago, or further species await formal taxonomic description). We adopted a conservative approach and used the total number of sampled lineages in each study (regime-A) as the number for each clade, instead of taking the total number recorded in each archipelago for each lineage (regime-B) as greater phylogenetic sampling may reveal these clades to be polyphyletic. For plants, we assessed for differences between regime-A and regime-B by comparing diversification rates obtained from both. For regime-B, the total number of species per archipelago was obtained from the World Checklist of Vascular Plants (WCVP, http://wcvp.science.kew.org), with the archipelago delimited based on the International Working

Table 1 Types of variables recorded from publications investigating the phylogenetic relationships of Pacific taxa and the limitations of the variables

Variable	Description	Limitations
Taxon	The taxon investigated. Where large groups of organisms were investigated, the taxon was sometimes split into various smaller taxa (all taxa analyzed were below the family level). For example, the different genera in the family Podocarpaceae were considered separate taxa.	The circumscription of a taxon analyzed in a study is determined by the researcher and hence subjective. The sampling of the taxonomic units within a taxon can be incomplete.
Family	Family of the taxon.	N/A
Phylum	Phylum of the taxon (Animalia or Plantae).	N/A
Target archipelago	Refers to the archipelago on which the colonization event occurred. We retained data for 16 archipelagos (Table 2) for which data for more than 20 colonization events (see Fig. 1 for sample size) was available.	N/A
Source of the colonization event	The inferred source of the colonization event. This was usually considered to be either the archipelago with the most closely related lineage or the archipelago hosting the lineage sister to that of the "target archipelago", with the interpretation following the suggestions by the authors where available.	Incomplete sampling means that the actual source for the colonization event could be a taxonomic unit that was not sampled or one that has become extinct.
Lineage source	The inferred source of the lineage that colonized the Pacific. These are generally one of the following mainland areas: Africa, America, Asia, Australia, and Malesia. Some lineages were inferred to have originated within Melanesia or Polynesia.	Incomplete sampling means that the source for the colonization event could be a taxonomic unit that was not sampled or one that has become extinct.
Stem age	The age of the stem of radiation on an archipelago. It was taken to be the age of divergence from the closest relative outside the archipelago if only a single taxon was sampled from an archipelago.	If a group has incomplete sampling or the molecular clock is incorrectly calibrated, published estimates may be incorrect.
Crown age	The age of the crown in taxa for which radiation (diversification into two or more species) occurred in an archipelago.	As for stem age.
Estimated age	This was the best age estimate based on the provided data, being either the average of the stem and crown ages (see above) or the stem age, if the taxon did not speciate on the archipelago.	Derived from stem and crown ages (see above for limitations). Stem age can over- or underestimate colonization time (García-Verdugo et al., 2019).
Colonization ratio	The proportion of radiations that are the result of a single colonization event (i.e., form monophyletic or paraphyletic groups, as opposed to being polyphyletic). A minimum of two taxmic units needed to have been sampled for the taxon to be included in this ratio.	Incomplete sampling inside and outside of the target archipelago could strongly impact this parameter.
Loci used	The loci or part of the genome used in the reference to infer the phylogeny.	The number and type of loci used will affect the phylogeny that is produced. Few loci may provide a poorly resolved tree and loci from different parts of the genome (e.g., nuclear vs. organellar) may produce conflicting results.

N/A, not applicable.

Group on Taxonomic Databases for Plant Sciences (TDWG3, “botanical countries”; Brummitt et al., 2001). We show that diversification rates obtained from both regimes were significantly correlated ($P < 0.0001$; Table S2), hence providing confidence that our results are robust to incomplete sampling based on phylogenetic data. For animals, regime-B was not available. We also tested for significant differences in diversification rates between plants and animals across archipelagos, as these differences were nonsignificant apart from New Caledonia (Fig. S1), we combined both data sets in our analyses.

2.4 Statistical analyses

For each archipelago, we tested whether the proportion of colonization events from a source area decreased with the geographical distances between the sources and the archipelago. Tests were performed separately for each archipelago using linear models and with all archipelagos using mixed-effect linear models (with the source's identity as a random factor affecting the intercepts) using the *lme4* R package (Bates et al., 2022). Distances and proportions of colonization events were log-transformed before fitting the models. As the proportions of colonization events from the different source areas included null values (45 among the 128 observations), we added 1 to the proportions before log-transformation.

For each colonization event, the distance to the closest source area was computed using the *sf* R package (Pebesma, 2018) as the distance between the centroid of the target archipelago and the closest coastline of the source area. When a target archipelago was nested in the source area, we used the distance between the target archipelago and the closest archipelago within the source area. For instance, for the distance between the archipelago of Fiji and the source area of Melanesia, we used the distance between the centroid of Fiji and the closest coastline of the Vanuatu archipelago.

To compare diversification rates across archipelagos, we performed Kruskal–Wallis tests using the R package *rstatix* (Kassambara, 2021). Subsequent *post hoc* Dunn's tests were conducted to determine which regions differed significantly from each other. Bonferroni *p* adjustments were selected for these Dunn's tests. Diversification rates were log-transformed prior to analysis.

To test whether diversification rates were correlated with (i) total terrestrial area of each archipelago, (ii) age of an archipelago (Table 2), or (iii) degree of isolation, Spearman rank tests were conducted with our filtered diversification data set containing individual lineages across all eight archipelagos. For each archipelago, an isolation index was computed as the sum of the distances to the different source areas weighted by the proportion of colonization events coming from those areas. All variables were log-transformed prior to analysis.

3 Results

3.1 Sources

We collected data for a total of 777 colonization events from 16 archipelagos for 118 plant and 69 animal lineages (Table S1). The sources of lineages were predominantly found to be the closest continental landmass (Fig. S2). The actual colonization events generally occurred from a source in close proximity (Fig. 1). For example, while biota on Lord Howe Island and New Caledonia originated mostly through colonization from Australia, that of the Galapagos is mostly sourced from the American continents. The proportion of taxa in an archipelago originating from a particular source area was strongly and negatively related to the distance of that archipelago from the source area (Fig. 2, marginal $R^2 = 0.39$, conditional $R^2 = 0.58$, $P < 0.001$). This was true for all source areas except Micronesia.

3.2 Age

For most archipelagos, recent colonization events (<5 Mya) were prevalent (Fig. 3). Overall, 66.8% of all recorded colonization events dated to less than 5 Mya (Fig. S3). However, for two of the oldest archipelago, New Caledonia and Fiji, a lower proportion of colonization events were of recent origin (i.e., the violin plots are more elongated and less bottle-shaped). The phylogenetic age estimates for taxa often corresponded well with our geological knowledge of islands (Fig. 3). However, for the Galapagos, Hawaii, Lord Howe, Marquesas, Society Islands, and Samoan archipelagos, phylogenetic data suggested considerably earlier colonization events than the age of the emergent oldest island. For the Austral Islands, Cook Islands, and Vanuatu archipelagos, the estimated ages for colonization events were younger than the estimated ages based on geological data.

3.3 Diversification

The proportion of lineages on an archipelago that result from a single colonization event is greatest on the most isolated islands and lowest on the islands that are closest to continental source areas (Fig. 1). After filtering for data sets suitable for estimates of diversification rate (see methods for criteria), 147 datapoints across eight archipelagos were retained for stem age and 115 datapoints were retained for crown age using a combined data set (plants and animals). Lineages on the oldest islands of New Caledonia and Fiji had the lowest median stem diversification rates ($P < 0.01$), followed by the Galapagos and Hawaiian archipelagos (Fig. 4). The lineages from younger, Polynesian islands had higher diversification rates than those from Melanesia and the Galapagos Islands (Fig. 4). Interestingly, Hawaii had the lowest median diversification rate across the four included Polynesian archipelagos. The Solomon Islands lineages have the greatest range in diversification rates and, hence, its ranking shifts across different diversification regimes (with either no extinction or high extinction rates), and this explains why it has a higher median diversification rate than the other Melanesian islands, with a median rate more similar to Polynesian islands. Only New Caledonian lineages had significantly different diversification rates from other archipelagos, based on *post hoc* Dunn's tests. A similar trend was observed for crown diversification rates, with Polynesian lineages having higher rates than Melanesian ones, with lineages in Fiji and New Caledonia having the lowest diversification rates (Fig. S4). Across archipelagos, diversification rates were negatively correlated with both area and archipelago age ($P < 0.0001$; Table S3).

Table 2 The 16 archipelagos that were included in the analysis and the ages assigned to each with reasons based on geological and tectonic histories

Archipelago	Age (Mya)	Explanation of age used	Source
Austral Islands	12.2	We took the age of Rurutu, the oldest island with an elevation >100 m. The oldest island in this hotspot archipelago is Rimatara, which emerged 25.1 Mya.	Clouard et al. (2005)
Bismarck Archipelago	23	The archipelago reportedly followed a similar developmental process as the Solomon Islands archipelago.	Hall (2001)
Caroline Islands	14.8	Because the oldest rocks in the Palau archipelago (maximum of 20 Mya) are overlaid by limestone, indicating subsequent submersion, we based the age on the next oldest archipelago (Chuck; maximum 14.8 Mya).	Neall & Trewick (2008); Rehman et al. (2013)
Cook Islands	19.4	We use the age of the oldest emergent island.	Clouard et al. (2005)
Fiji	28	While older rocks are present on Viti Levu, we here consider the commencement of a major volcanic phase 28 Mya as the start of the Fiji archipelago.	Neall & Trewick (2008)
Galapagos	3	The oldest islands in the archipelago emerged in about 3 Mya, but some submerged seamounts extend back to 14 Mya.	Neall & Trewick (2008)
Hawaii	5.1	We use the age of the oldest major emergent island, Kauai, although the Kure Atoll formed 25 Mya.	Neall & Trewick (2008)
Lord Howe	6.4	We use the end of volcanic activity.	McDougall et al. (1981)
Mariana Islands	3	We use the time when the uplift of the archipelago began and exposed considerable terrestrial areas—small islands may have existed prior to this.	Tracey Jr et al. (1964)
Marquesas	5.5	We use the age of Eiao, the oldest island in this hotspot archipelago.	Clouard et al. (2005)
New Caledonia	33	While New Caledonia is an old continental fragment, it only re-emerged after a complete submersion, not more than 33 Mya.	Cluzel et al. (2012)
Samoa	2.3	We use the date for the oldest island, ‘Upolu, in this hotspot archipelago.	Clouard et al. (2005)
Society Islands	4.2	We use the emergence of Maupiti, the oldest emergent island of this hotspot archipelago.	Clouard et al. (2005)
Solomon Islands	23	We use the oldest date provided for the collision of the Solomon Arc with the Ontong Java Plateau. Although exposed rocks on some islands date back to before this time, the collision had a profound impact on the formation of the archipelago.	Petterson et al. (1999); Neall & Trewick (2008)
Tonga	17	We use the end of the most recent volcanic activity on ‘Eua, the oldest island in the archipelago, as it overlays older volcanic events.	Hoffmeister (1932); Duncan et al. (1985)
Vanuatu	22	We use the age of the oldest islands, Espiritu Santo and Malekula.	Green & Wong (1988)

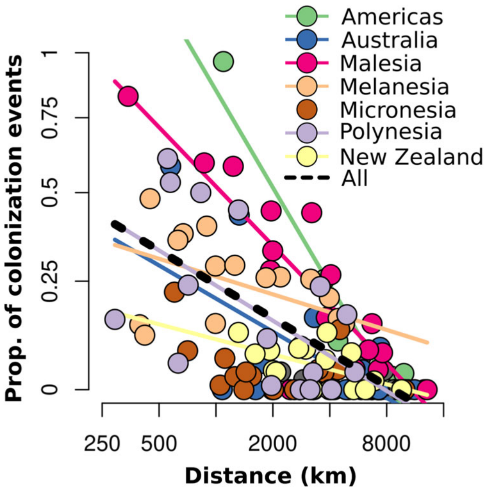

Fig. 2. Relationships between the proportion of colonization events contributed by a source area with the distance between that source area and the colonized (target) archipelago. Trendlines indicate significant ($P \leq 0.05$) relationships for six of seven (Asia was excluded because of small sample sizes) source areas, separately. Only Micronesia did not display a significant relationship. The black dotted line indicates the significant overall trend ($P < 0.001$).

4 Discussion

The probability of Pacific Islands experiencing a colonization event is strongly dependent on the distance to source pools for biota and this tendency is possibly best illustrated by the steadily waning influence of the American, Australian, and Malesian source areas on the biota of Pacific archipelagos with increasing distance (Figs. 1, 2). Furthermore, on most archipelagos the majority of colonization events occurred in the more recent history of an archipelago, suggesting that most of the biota for all but the oldest archipelagos (Fiji and New Caledonia) originated less than 5 Mya (Fig. 3). Diversification rates were highest on younger islands, possibly suggesting that more niches are already occupied on older islands (Fig. 4). Overall, our results are consistent with expectations based on the taxon cycle. However, a lower proportion of recent arrivals and lower diversification rates on older archipelagos suggest that the taxon cycle may slow as archipelagos age.

4.1 Taxon cycle

Our findings broadly support the concept of the taxon cycle, which posits that islands are in a state of constant flux as new taxa that are mostly ecological generalists and good dispersers establish and displace earlier colonizers to habitats located further inland (Wilson, 1961; Pepke et al., 2019). Our data support that the ongoing establish-

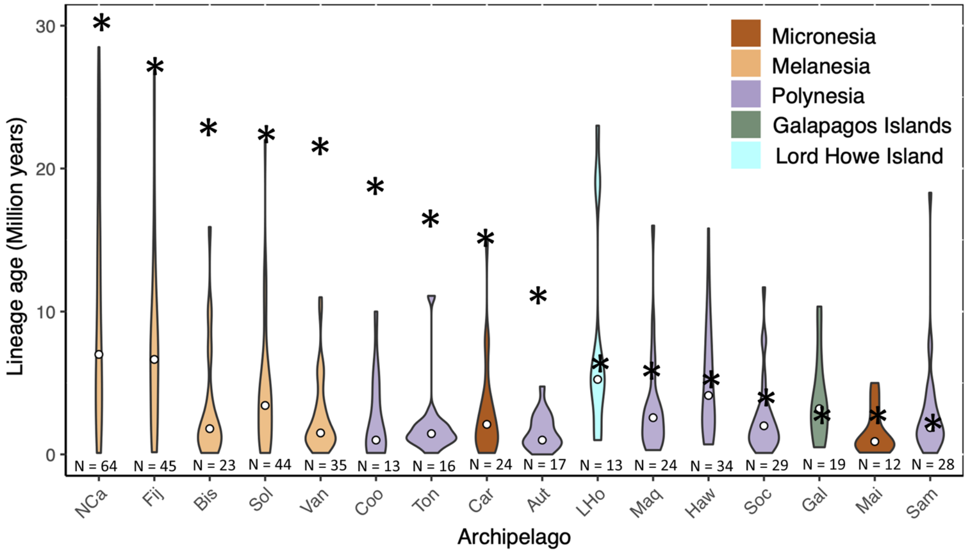

Fig. 3. Violin plots of the estimated ages of lineages (see Table 1 for definition) based on dated colonization events and asterisks for the estimated conservative ages of archipelagos (asterisks, see Table 2 for the reasoning behind applied age estimate) for 16 archipelagos in the Pacific. Note that the age for New Caledonia was estimated at 33 Mya but plotted as 30 Mya for easier visualization. Archipelagos are arranged by decreasing age from left to right. The width of each violin plot indicates the density of values (Hintze & Nelson, 1998) for each age, and the white circle the value of the median. Violin plots are colour coded for the region each archipelago occurs in (c.f. Fig. 1). Aut, Austral Islands; Bis, Bismarck Archipelago; Car, Caroline Islands; Coo, Cook Islands; Fij, Fiji; Gal, Galapagos Islands; Haw, Hawaii; LHo, Lord Howe Islands; Mai, Mariana Islands; Maq, Marquesas; *N*, number of aged colonization events included; NCa, New Caledonia; Sam, Samoa; Soc, Society Islands; Sol, Solomon Islands; Ton, Tonga; Van, Vanuatu.

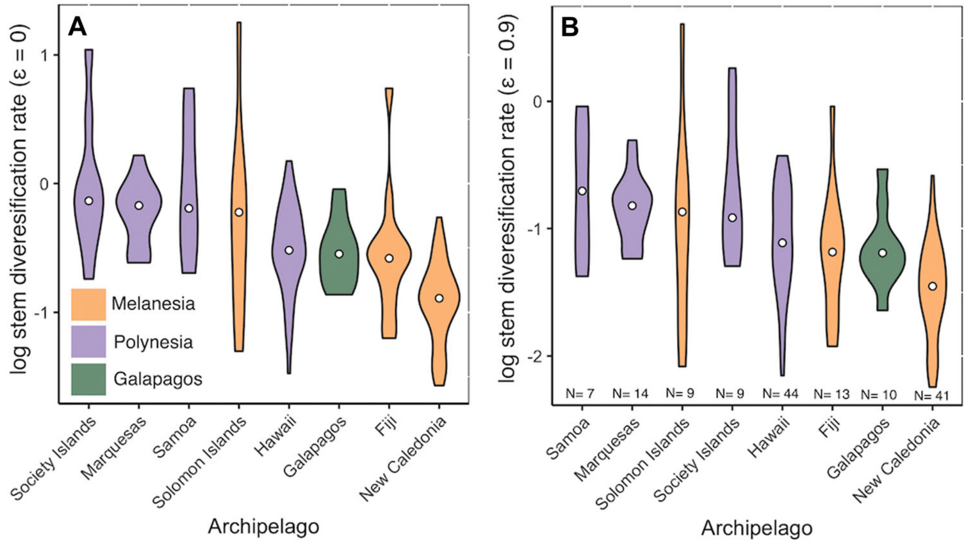

Fig. 4. Violin plots showing logged stem diversification rates per Archipelago with (**A**), no extinction (i.e., pure birth, ε = 0), and (**B**), high extinction fractions (ε = 0.9). The width of each violin plot indicates the density of values (Hintze & Nelson, 1998) for each age, and the white circle the value of the median. Archipelagos are arranged from high to low (median). Violin plots are colour coded for the region each archipelago occurs in (c.f. Fig. 1). *N*, number of aged colonization events included.

ment of new colonizers is common, as most colonization events are of very recent origin (Fig. 3) and colonizers tend to originate from the closest source areas (Figs. 1, 2). Widespread taxa with little genetic differentiation have been reported across a wide range of taxonomic groups, such as birds (Andersen et al., 2015), cycads (Liu et al., 2021), and snails (Lee et al., 2014). Additional support for the taxon cycle comes from molecular studies of selected Pacific taxa, including ants, birds, and lizards, which report a pattern of more recent colonists in coastal areas and earlier colonists occupying inland habitats (Economo & Sarnat, 2012; Matos-Maraví et al., 2018; Oliver et al., 2018; Pepke et al., 2019). Studies have also shown that good dispersers can colonize archipelagos frequently and repeatedly (Andersen et al., 2013; Johnson et al., 2017).

However, the oldest two archipelagos (New Caledonia and Fiji) in our data set diverge from the general trends observed. A much lower proportion of colonization events on these archipelagos (compared to the younger archipelagos) is of recent (<5 Mya) origin, suggesting a lower number of recent, successful colonization events. There are two potential explanations for this observation. First, these older islands could be receiving a lower number of propagules. However, this is unlikely based on prevailing ocean currents and wind directions (Liu et al., 2021; Demeulenaere & Ickert-Bond, 2022). It is, therefore, more likely that these older islands receive a similar number of propagule arrivals but that chances of establishment are lower.

We suggest that the reduced number of successful colonizations may be due to a greater number of niches being already filled on those islands (Fritz et al., 2012). Greater niche filling would interfere with the establishment of taxa on islands, particularly during the second stage of the taxon cycle when colonizers adapt to inland habitats. It has indeed been suggested that niches become increasingly filled during island ontogeny (Whittaker et al., 2008; Borregaard et al., 2016). Therefore, ecological-evolutionary theory predicts a slowing of the taxon cycle because archipelagos accumulate species and functional diversity with age, which pre-empts niche space, limiting opportunities to adapt and speciate (Yoder et al., 2010; Gillespie et al., 2020). Furthermore, populations that remain small and/or isolated, because of limited niche space being available, are more vulnerable to decline and extinction (Frankham, 1998; Harter et al., 2015; Saatkamp et al., 2018). Similarly, greater diversity has been linked to reduced invasibility of communities (Zhang et al., 2020; Li et al., 2022).

The concept of a slowing taxon cycle, therefore, may allow for a more complete understanding of island biogeography, especially if combined with the theory of island biogeography, which proposes that species diversity is mostly determined by the age, area, and isolation of an island (MacArthur & Wilson, 1963, 1967; Whittaker et al., 2008). While the theory of island biogeography is readily applicable to islands within an archipelago (Whittaker et al., 2008; Carey et al., 2020, 2023), regional effects are also known to influence species diversity (Rosenzweig & Ziv, 1999; Ibanez et al., 2018). The taxon cycle offers mechanisms to account for such regional effects, explains the dynamic nature of species composition (Morrison, 2010; Keppel et al., 2014), and highlights that archipelagos in the Pacific are both cradles and graves of biodiversity.

While our findings support the taxon cycle as a good mechanistic model to explain current patterns of biodiversity in the tropical and subtropical South Pacific at the archipelago level and suggest that the process slows late (after c. 20 Mya) in an archipelago's life, many unanswered questions remain. While evidence for the taxon cycle has also been reported from the Caribbean (e.g., Ricklefs & Bermingham, 2002), one would expect the concept to be less relevant on nonoceanic islands, such as tropical continental shelf archipelagos with islands that formed due to rising sea levels after the last glacial maximum. Such islands would already have limited available niche space upon formation (Ali, 2018). Although the signal for a slowing taxon cycle is strong in our data set, with the three older archipelagos, Fiji, New Caledonia, and the Solomon Islands, displaying a much lower proportion of recent colonization events than the younger archipelagos, our data set is opportunistic with unequal and incomplete sampling of taxa and archipelagos. Therefore, the slowing of the taxon cycle on older, large islands should be further tested using more complete data sets and different study areas.

Furthermore, the mechanisms driving the processes within and across various stages of the taxon cycle should be further explored. While the importance of interspecific competition in defining realized niche spaces (Faaborg, 1980; Naikatini et al., 2022) and the potential of new colonists to displace existing species (Case et al., 1994; Kamath et al., 2020) have been demonstrated for islands, the relative importance of competitive displacement in driving the taxon cycle has not. Other processes, such as hybridization, could play a key role in facilitating adaptation to new environments by colonists (Johnson et al., 2019; Gillespie et al., 2020; Linan et al., 2022) and causing the extinction of existing taxa (Keppel et al., 2011; Lawson et al., 2017).

4.2 Sources

Our findings suggest that the proximity of source areas is the most powerful predictor of where the biota of an island originates (Fig. 1). Only Micronesia was not always as prominent a source area as suggested by the distance of the receiving archipelago (Fig. 2), possibly because of the strong influence of the highly diverse Malesian source area (Fig. 1). Therefore, it seems more appropriate to focus on archipelagos or regions, rather than the whole Pacific, when discussing source areas in the tropical and subtropical Pacific. Our results support major source areas previously reported for some of the archipelagos, including Malesia for those in Melanesia (Keppel et al., 2009) and Micronesia (Demeulenaere & Ickert-Bond, 2022), Australia for New Caledonia (Keppel et al., 2009; Nattier et al., 2017), and the American continents for the Galapagos (Parent et al., 2008). In addition, they support the diverse nature of source areas for the biotas of Hawaii (Price & Wagner, 2018) and the Marquesas (Hembry, 2018).

Furthermore, our findings support the Pacific Islands as important source areas for colonization events in the Pacific, which has been previously reported for the Hawaii and Marquesas archipelagos (Hembry, 2018; Price & Wagner, 2018). Our analyses suggest that islands within the Pacific can contribute more than 50% of the successful colonization events (Fig. 3) that formed the biota of archipelagos in the central Pacific. Furthermore, the values presented here likely underestimate the role of colonization from within the Pacific, as islands from the Pacific, particularly those in Melanesia, are often undersampled in phylogenetic studies (Keppel et al., 2009, 2021). Of particular interest from an evolutionary viewpoint is that there is an increasing number of lineages believed to have arisen in the Pacific, including the snake family Hydrophiinae (Strickland et al., 2016), the snail family Patulidae (Lee et al., 2014), and the Melanesian clade of the plant genus *Schefflera* (Plunkett & Lowry II, 2012). Furthermore, there is growing evidence that Pacific Islands have served as source areas for continental flora, as exemplified by the plant genus *Planchonella* (Swenson et al., 2019) and the bird genus *Monarcha* (Filardi & Moyle, 2005).

It should be noted that the proximity and size of landmass for different archipelagos, which were never connected (Hall, 2002), would have differed through time as sea levels rose and fell (Neall & Trewick, 2008). In addition, the Melanesian islands, including Fiji, were in closer in proximity between about 30–10 Mya as part of the Caroline and Melanesian Arcs before becoming further separated by geological processes (Hall, 2002). The importance of this greater proximity among the different Pacific archipelagos in facilitating the dispersal and, hence, divergence of taxa has been suggested based on the molecular results of several studies (Lucky & Sarnat, 2010; Jønsson et al., 2018; Oliver et al., 2018). Furthermore, the directionality of dispersal, which was not investigated in this study and is driven by the directions of prevailing ocean currents and winds, likely influences the proportional contributions of various source areas to the floras of archipelagos (Sanmartín et al., 2007; Grudinski et al., 2014). Other factors, such as bird flyways and prevalent cyclone paths may also affect the relative importance of different source areas (Larrue, 2014; Demeulenaere & Ickert-Bond, 2022).

4.3 Archipelago age

Generally, there was good correspondence between the molecular age estimates of colonization events and the geological age estimates for archipelagos (Fig. 3). However, for two scenarios the molecular dates were older than the geological age estimates for the oldest emergent island. First, the Galapagos, Hawaii, Marquesas, Society Islands, and Samoan archipelagos are hotspot archipelagos that have older, now submerged islands. For example, the Galapagos and Hawaii archipelagos have submerged islands that date to 14 and 25 Mya, respectively (Neall & Trewick, 2008), meaning part of the biota could have arrived on these now submerged islands before dispersing to the younger islands within the archipelago. Indeed, several dispersal events in Hawaii have been dated molecularly to be older than the oldest currently emerged major island, Kauai (e.g., Cognato et al., 2018; Swenson et al., 2019).

In addition, Lord Howe Island and New Caledonia have components of their biota for which the separation from their closest sister taxon considerably predates the origin of the archipelagos' landmass (see also Nattier et al., 2017). For example, for the genus *Planchonella* in New Caledonia and the Lord Howe stick insect, separation from Australian sister taxa was dated to at least 39 (Swenson et al., 2019) and 19 Mya (Buckley et al., 2009), respectively. This could be interpreted as support for panbiogeographic theories that invoke persistence over millions of years on older, now submerged islands (Heads, 2010). However, both of these archipelagos are relatively close to Australia, which supported much wetter climates until about 5.5 Mya. These older lineages may hence have had now-extinct ancestors on the Australian continent before the decline of its rainforest biome (Byrne et al., 2011). In other words, the older stem ages of selected lineages compared with the age of emergent islands may also be the result of the extinction of sister lineages.

Almost two-thirds of our recorded colonization events occurred less than 5 Mya, indicating that most of the Pacific flora is of relatively recent origin. This finding, together with the good correspondence between molecular colonization ages and geological age estimates and the lack of concrete evidence for any colonizations via vicariance (e.g., drifting into the Pacific on continental landmasses), suggests dispersal as an (almost) universal mechanism of colonization for islands in the South Pacific, as has been previously suggested (Keppel et al., 2009; Nattier et al., 2017). Studies on Pacific archipelagos outside the tropics and subtropics have arrived at similar conclusions (Pole, 1994; Winkworth et al., 2005; Nge et al., 2021).

4.4 Diversification

Diversification rates were significantly and negatively correlated with archipelago age and area, despite species richness displaying the expected and well-documented positive correlation with these variables (MacArthur & Wilson, 1963; Keppel et al., 2009, 2016). This suggests that time for species accumulation and greater environmental heterogeneity are more important drivers than elevated diversification in explaining disparities in species richness across Pacific archipelagos. The importance of evolutionary time for species accumulation has been documented not only for island systems (e.g., Meudt et al., 2021) but also across other regions and systems (Wiens et al., 2011; Li & Wiens, 2019; Nge et al., 2020). Higher diversification rates on younger, albeit smaller, archipelagos could result from the presence of new uncolonized ecological niches—that facilitate radiation. The potential for radiations to fill available niche space has been well documented (e.g., Gillespie, 2004). Incorporating ecological traits with denser phylogenetic sampling across different scales would allow testing of this hypothesis (Cerca et al., 2023; Johnson, 2023).

Interestingly, the range of diversification rates found in Hawaii and the Galapagos are similar to those from other Pacific archipelagos included in this study (with the exception of New Caledonia, which has significantly lower rates). These two archipelagos have been extensively studied, with iconic adaptive radiations noted such as the Galapagos finches (Román-Palacios & Wiens, 2018), Hawaiian silverswords (Baldwin & Sanderson, 1998), lobeliads (Givnish et al., 2009), and songbird radiations (Fleischer et al., 2022). However, it is worth noting that adaptive radiations refer to the divergence of lineages into different ecological niches, and this may not necessarily be associated with elevated diversification rates (Rundell & Price, 2009; Givnish, 2015). A holistic approach is required to compare these differences instead of focusing on selected case studies such as the aforementioned charismatic groups. Indeed, we show that other Pacific archipelagos, many of which remain under-studied, have higher mean diversification rates than Hawaii or the Galapagos. Adaptive radiations, and whether they are coupled with elevated diversification rates, should be investigated in these other archipelagos (Cerca et al., 2023).

Results for the Solomon Islands are of particular interest. This archipelago has lineages with higher diversification rates than other Melanesian archipelagos, with the median diversification rate being more like lineages from Polynesia. The Solomon Islands are one of the most species-rich and oldest (~23 million years old) archipelagos in the wider Pacific (Keppel et al., 2010). Coupled with the archipelago's relatively low colonization ratio (Fig. 1), this suggests that the present-day species richness of the Solomon Islands resulted from a combination of high diversification rates and radiations of selected lineages, time for the accumulation of lineages, and repeated colonization from surrounding sources. The Solomon Islands archipelago is also unique in the tropical South Pacific in having several larger islands (seven islands exceed 3000 km^2 in area: Bougainville, Choiseul, Guadalcanal, Malaita, Makira, New Georgia, and Santa Isabel). Therefore, the chances of lineages evolving into separate species on different islands may be greater (e.g., Andersen et al., 2013; Johnson et al., 2019). Whether lower extinction rates, greater proximity and connection to other landmasses, or larger areas are the main factors producing the unique phylogenetic history in the Solomon Islands is a topic worth pursuing further, especially because our data set only included radiations for nine lineages.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.13026/suppinfo:

Table S1. Taxon (including family (or higher taxon) and phylum (Phy)), target archipelago (TArch), source area, ancestry of lineage, stem and crown age, number of operational taxonomic units (OTUs) included, loci surveyed, and reference source for 777 colonization events included in this study. A = Animalia, Aut = Austral Islands, Bis = Bismarck Archipelago, Car = Caroline islands, Coo = Cook Islands, Fij = Fiji, Haw – Hawaii, Gal = Galapagos Islands, LHo = Lord Howe Islands, Mai = Mariana Islands, Maq = Marquesas, NCa = New Caledonia, NMC = no molecular clock approach applied P = Plantae, Sam = Samoa, Soc = Society Islands, Sol = Solomon Islands, Ton = Tonga, Van = Vanuatu.

Table S2. Spearman rank correlation tests between diversification rates calculated from regime-A (number sampled per clade) and regime-B (total species recorded per Archipelago based on the Kew plant checklist) for plants. '*' indicates significant correlation (p value). 'ε' represents relative extinction fraction for the diversification rate metric.

Table S3. Summary statistics for diversification rate correlates with area size, archipelago age.

Fig. S1. Boxplots showing diversification rates of animals and plants across all sampled Archipelagos after filtering. * indicates significant ($p < 0.05$) differences between groups. 'n' indicates the sample size (number of lineages) in each group. Boxplots represent the interquartile range with the central horizontal bar in each box showing the median, and white dot showing the mean. Whiskers show location of most extreme data points that are still within a factor of 1.5 of the upper and lower quartiles, and black points show outliers outside this range.

Fig. S2. The sources of lineages for 16 focal archipelagos in the tropical and subtropical South Pacific. The pie charts indicate the proportion of colonization events originating in the various color-coded source areas.

Fig. S3. Ages of 440 colonization events in relation to their estimated age. Data was extracted from literature (see Table S1).

Fig. S4. Violin plots showing logged crown diversification rates per Archipelago with A, no extinction (i.e., pure birth, $\varepsilon = 0$), and B, high extinction fractions ($\varepsilon = 0.9$). The width of each violin plot indicates the density of values (Hintze & Nelson, 1998) for each age and the white circle the value of the median. N = number of aged colonization events included. Archipelagos are arranged from high to low (median).