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RESEARCH ARTICLE

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Beta-diversity within coral atolls: Terrestrial species turnover increases with cyclone frequencies

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Abstract

Aim: Atolls are a widely distributed, common type of tropical ecosystem, each consisting of an annular coral reef and up to several hundred individual islets sitting on the reef platform. The small land areas and low elevation render the terrestrial communities susceptible to local extinctions from overwash and inundation due to tropical cyclones. Such recurring catastrophic disturbances should be expected to drive strong priority effects and historical contingency in species assembly, thus also promoting species turnover within atolls. This stands contradictory to the received wisdom of atolls consisting of numerous uniform, replicated island systems. We tested the hypothesis that the individual islets within an atoll exhibit compositional turnover and that this species turnover within atolls is related to cyclone frequency.

Location: Atolls worldwide.

Time Period: Present.

Taxa Studied: Vascular plants, reptiles, birds.

Methods: We compiled a global dataset at the level of islets for species presence/absence within atolls. We obtained long-term (80 year) tropical cyclone frequency data for each atoll from the NOAA hurricane database and used Bayesian regression to estimate the effects of tropical cyclone frequency on species turnover within atolls.

Results: We consistently measured high within-atoll species turnover (i.e., between the individual islets within an atoll) on atolls worldwide. The degree of within-atoll species turnover increases with increasing tropical cyclone frequency. Atolls that are more frequently hit by tropical cyclones show higher species turnover between their islets than those that occur outside the tropical cyclone belt.

Main Conclusions: Tropical cyclones are a significant driver of the community assemblages on atolls. These catastrophic disturbances promote a heterogenous atoll landscape, which challenges perceptions that the islets within an atoll are identical replicates of the entire atoll terrestrial community. Biodiversity surveys undertaken at the islet-level (alpha-diversity) might therefore not be representative of the entire atoll metacommunity (gamma) diversity.

KEYWORDS
atoll, beta-diversity, colonization, hurricanes, island biology, species assemblage, typhoon

1. INTRODUCTION

Atolls are unique tropical ecosystems, formed by an annular coral reef that encloses a central lagoon, and up to several hundred individual islets sitting on top of the reef platform (Woodroffe & Biribo, 2011). There exist 321 atolls with permanently emerged land area, distributed across the tropical to subtropical Indian, Pacific, and Caribbean oceans (Goldberg, 2016). Throughout the Indo-Pacific oceanic basin, atolls are at least as common and numerous as high volcanic islands, but compared to high islands, the low-lying and small atoll islets have low levels of endemism and relatively depauperate floras and faunas (Nunn et al., 2016). Nevertheless, most atolls fall within one of the global biodiversity hotspots (Myers et al., 2000), and their islets house breeding colonies of global significance for various tropical seabird species (Berr et al., 2023), and other emblematic Pacific Island species (Lee, 1984).

Among the most prominent features of atolls is the annular arrangement of their islets, which total from just one to several hundred individual islets per atoll (Woodroffe & Biribo, 2011). The islets within an atoll are formed from loose deposits of reef sediments and separated from one another by channels (Johnson & Ortiz, 2023; Morgan & Kench, 2016). Each islet within an atoll therefore undergoes its own process of terrestrial species colonization, succession, and community assembly (Bayliss-Smith, 1988). Given the overall remoteness and uniformity in environmental conditions, the individual islets within a given atoll are often assumed to house largely the same sets of terrestrial species as the entire atoll. This is reflected in the thinking of atoll islets as 'replicate islands' in the framework of control-impact ecosystem studies (e.g., Graham et al., 2018; Steibl et al., 2022). However, this is a largely untested assumption.

The small land areas, high isolation, and lack of elevational gradients of atoll islets suggest a rather uniform and predictable species assembly on the global scale, and in comparison to large oceanic islands (Kreft et al., 2008). At the same time, these same factors also render atoll islet communities susceptible to local extinctions (extirpations) (MacArthur & Wilson, 1967). The predominant type of natural catastrophic disturbance on atolls is tropical cyclones (regionally also called hurricanes or typhoons), which frequently over-wash or completely inundate atoll islets and thereby can cause local extinctions of terrestrial species (Duvat et al., 2017; Ford & Kench, 2016; Stoddart, 1971). Therefore, recurring tropical cyclones would be expected to promote strong priority effects and historical contingency in terrestrial community assembly on atolls (Fukami, 2015).

The effects of tropical cyclones as environmental drivers for species assemblages in various ecosystems are well established (Lin et al., 2020; Morrison & Spiller, 2008). Depending on the ecological context, tropical cyclones can have homogenizing or non-homogenizing effects on community composition (Worthy et al., 2021). Homogenizing effects can arise due to selective, deterministic mortality/survival (McCoid, 1996), a reduction in environmental heterogeneity (Comita et al., 2010), and synchronized succession trajectories following the disturbance event (Xi et al., 2019). Non-homogenizing effects can be caused by an increase in environmental heterogeneity, stochastic extinction processes, or asynchronous recovery rates (Schoener & Spiller, 2006). These effects on community composition are quantified through beta-diversity, and in particular, its turnover component, that is, the replacement of species between sites. Tropical cyclones can also control the nestedness component of beta-diversity, that is, species richness differences between sites, when species extinctions are deterministic (Bloch et al., 2006; Morrison, 2013).

Within an atoll, cyclone impacts are not uniform but heterogeneous, as they are commonly concentrated at a subset of an atoll's islets, and usually stronger on those facing the windward side or laying directly within the cyclone track (Ford & Kench, 2016). For example, a detailed analysis of tropical cyclone *Ophelia* on Jaluit atoll (Marshall Islands) in 1958 found that during its passing over the atoll, some islets of the atoll were submerged to a depth of 1.8 m, destroying 90% of the vegetation cover and causing several local extinctions, while other islets within the same atoll barely flooded and suffered only minimal damage (Blumenstock, 1958; Blumenstock et al., 1961). These and observations from other atolls suggest that, over time, recurring tropical cyclones should increase compositional dissimilarity on islets within atolls due to localized extinction, re-colonization, and species assemblage processes (Stoddart, 1963, 1964; Stoddart & Walsh, 1992).

Tropical cyclone frequency varies across the tropical Indo-Pacific and Caribbean (Basconcillo et al., 2021) and atolls are widely distributed both within and outside the tropical cyclone belts with different encounter rates even within archipelagos (Duvat et al., 2020). If tropical cyclones are a major driver of compositional dissimilarity between the islets within atolls, then the within-atoll species turnover of atolls (i.e., between the different islets within one atoll) would be expected to increase with tropical cyclone frequency.

Our aim was to quantify beta-diversity and species turnover between the islets within atolls, and specifically test whether the degree of species turnover within atolls is correlated to their tropical cyclone encounter rate. We compiled a global dataset of islet-wise species occurrence (presence/absence) for vascular plants, reptiles, and birds. These three species groups comprise the native atoll macrofaunal and -floral communities, while amphibians and native mammals (except for fruit bats on few West Pacific and Indian Ocean atolls) are naturally absent. Native atoll invertebrate, lichen, and fungal communities are poorly catalogued, and we are not aware of any islet-wise species occurrence dataset for these groups. We quantified beta-diversity, species turnover and species nestedness for 29 atolls where survey data were available and obtained data on long-term tropical cyclone frequency for each atoll from the NOAA Historical Hurricane Tracks database. We then used Bayesian multilevel linear regression to estimate the effect of tropical cyclone frequency on terrestrial species turnover on atolls. We tested the hypothesis that within-atoll species turnover of atolls increases with tropical cyclone frequency, that is, the terrestrial communities on the different islets within an atoll are more dissimilar if the atoll is more frequented by tropical cyclones.

2. METHODS

2.1 | Data acquisition

We gathered literature on atoll terrestrial biodiversity and filtered for those reports where authors clearly stated that comprehensive cataloguing efforts were carried out on each islet within a given atoll. Species inventories with vague statements on species distribution across the islets of an atoll (e.g., 'present on most islets') were excluded. We also excluded data from elevated atolls, as the uplifting of atolls just 10–20 m above sea level already changes the stability and susceptibility to flooding or over-washing significantly (Stoddart & Walsh, 1992). Our final dataset was islet-wise species presence/absence data from 29 atolls (or roughly 10% of all atolls with permanently emerged land area in the world), comprising a total of 460 individual atoll islets (Figure 1). Our dataset includes atolls from across their entire range of occurrence, except for the Western Indian Ocean atolls and the atoll cays in the Banda Sea (see Goldberg, 2016 for an overview and map of the distribution of all atolls in the world). Our dataset includes biodiversity data for birds, both land and seabirds combined ($n=13$ atolls), vascular plants ($n=16$ atolls), and reptiles ($n=13$ atolls). We excluded all agricultural and ornamental pot plants (e.g., some authors listed planted tomatoes, watermelon or other vegetables that only survive in village gardens), as their occurrence on atolls is only possible with active cultivation and not the result of natural processes. Non-indigenous yet widely naturalized plant species on atolls were left included in the dataset (e.g., *Cocos nucifera*, *Morinda citrifolia*). Likewise, we excluded domestic bird species (e.g., domestic junglefowl *Gallus gallus*) from the dataset. We also excluded marine reptiles, that is, sea turtles, from the dataset. A reference list of the data sources used to compile the atoll biodiversity database can be found in the Supplementary Material.

We obtained data on tropical cyclone frequency from the Historical Hurricane Tracks database of the National Oceanic and Atmospheric Administration (NOAA), NOAA National Hurricane Center and NOAA National Center for Environmental Information (https://coast.noaa.gov/hurricanes, last accessed 17 Feb 2023). We extracted the number of tropical cyclones in storm category 1–5 that had passed each atoll within a 50 km radius (measured from the outer polygon of the atoll) over the entire available time range of the NOAA database (i.e., 1942–2021). Time scales of the biodiversity surveys on the atolls and the hurricane data are consistent and overlapping. We are not aware of any definitive threshold above which a tropical cyclone causes catastrophic damage on atolls (i.e., complete flooding and inundation), but reports on tropical cyclone impacts on atolls suggest passings within 70 km can cause the inundation of islets (Wiens, 1961). Our threshold of 50 km is thus a slightly more conservative distance to quantify the frequency of catastrophic impact on atolls that could drive local extinctions of terrestrial species. Data on atoll land area were taken from literature values published alongside the species list reports. The distance to the nearest high-volcanic island or continent was measured in Google Earth 10.40.0.2.

2.2 | Beta-diversity metrices

All data analysis was done in R 4.3.1 (R Core Team, 2021). For each of the $n=29$ atolls in our dataset, we computed beta-diversity (β_{SOR}) and its turnover (β_{SIM}) and nestedness (β_{SNE}) components across its islets and for each species group (plants, reptiles, birds), using the multiple-site Sørensen-based dissimilarity indices, implemented in the 'betapart' R package (Baselga & Orme, 2012). We computed β-values using the resampling procedure in the 'betapart'-package with 999 random samples to enable comparison of beta-diversity metrics between atolls (Baselga, 2010). As there exist numerous different computational algorithms for beta-diversity indices, we also calculated species turnover using the Podani and Baselga family Sørensen-based indices implemented in the 'adespatial' package (Dray et al., 2019) and tested for consistency among metrics. Spearman rank correlation indicated the robustness of the beta-diversity metrics across the different algorithms ($\rho=0.952$). We also combined the presence/absence matrices of the individual islets of each atoll into an atoll-level (gamma-diversity) community dataset

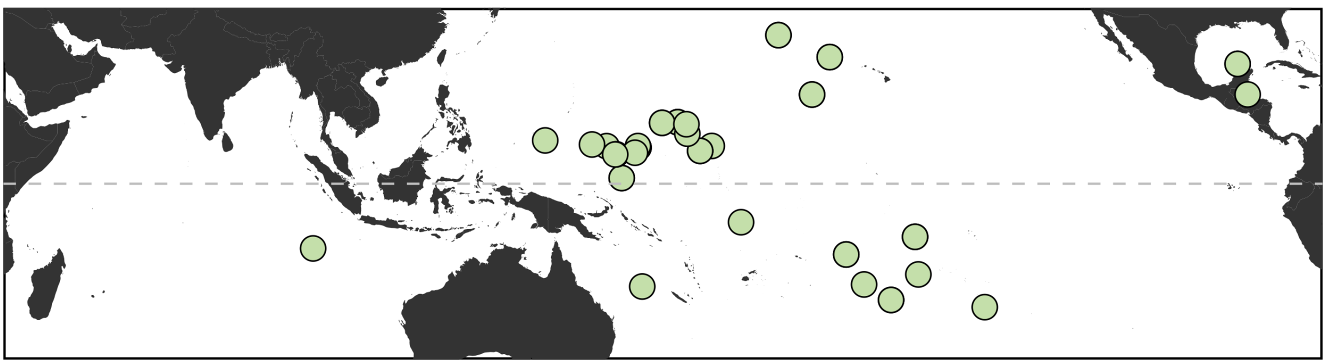

FIGURE 1 We obtained biodiversity data for 29 atolls in total (green points) across the Indo-Pacific and Caribbean basin, covering almost the entire distributional range of atolls worldwide (only atolls of the Western Indian Ocean and the Banda Sea were not included as no available species catalogue provided islet-wise occurrence data; see Goldberg (2016) and Nunn et al. (2016) for detailed maps displaying the geographic distribution of all atolls worldwide).

and calculated pairwise beta-diversity and its turnover component between the different atolls in our dataset.

2.3 | Bayesian regression analysis

For each atoll, the beta-diversity analysis provided one measure per species group for how dissimilar the communities between the different islets within a given atoll are. We estimated the effects of tropical cyclone frequency on this within-atoll species turnover β_{SIM} using a Bayesian linear regression framework with the 'brms' R package (Bürkner, 2017). As additional biogeographic covariates and potential factors influencing within-atoll species turnover, we also included 'number of islets', 'isolation' (distance to the nearest larger landmass), and 'total land area' per atoll as fixed effects, and 'atoll' as a random effect. All predictors were log-transformed to adjust for right-skewness in the distributions. The fixed effects were *z*-score standardized before the regression analysis. As turnover β_{SIM} is bound between 0 and 1, we specified a Beta response distribution with the default logit-log link function. We specified weakly informative logistic priors on the intercept (logit(normal(−0.5, 0.5))) and slope (logit(normal(0, 0.35))) parameters, and performed prior predictive checks, constructing four chains with 50,000 iterations minus a burn-in period of 25,000 iterations per chain. We evaluated model estimation by visually inspecting trace, trace rank, and autocorrelation plots, and by calculating Gelman-Rubin and Geweke-metrices. A summary of model validation metrics can be found in the supplementary results S1. We used the same framework to estimate the effect of tropical cyclone frequency on the second additive component of beta-diversity, the within-atoll nestedness $\beta_{SNE.}$

3. RESULTS

Overall, we detected high within-atoll beta-diversity across all investigated atolls and for all three major terrestrial species guilds (Figure 2). Average total beta-diversity β_{SOR} ranged from 0.51 for birds to 0.57 for plants, and its turnover component β_{SIM} from 0.24 for birds to 0.26 for reptiles. The average nestedness component β_{SNE} ranged from 0.27 for birds to 0.31 for plants. Overall, the within-atoll species turnover component was in the same range as the between-atoll species turnover for birds and reptiles, but plant species turnover was, on average, higher between atolls than within atolls (Table 1).

Tropical cyclone frequency varied between 0 and 13 cyclones passing within a 50 km radius of an atoll in the eight-decade period of available data (1942–2021). Tropical cyclone frequency had a significant positive effect on the within-atoll turnover (β_{SIM}) of plants [0.058, (0.002, 0.132)] ($p = 0.022$), reptiles [0.075, (−0.046, 0.257)] ($p = 0.027$) and birds [0.075 (−0.044, 0.247)] ($p = 0.016$). Neither total land area of an atoll nor distance to nearest larger landmass (isolation), nor the number of islets of an atoll had a significant effect on within-atoll species turnover (β_{SIM}) (Table 2, Figures 3 and S1). Tropical cyclone frequency, number of islets, distance to the nearest larger landmass, and atoll land area had no directional effect on the within-atoll nestedness component (β_{SNE}) of beta-diversity for plants, reptiles, or birds on atolls ($p > 0.05$ for all effects).

4. DISCUSSION

> The plant cover … is generally regarded [by others] as very uniform and uninteresting; however, this uniformity exists only in the minds of those who have visited very few atolls or who have observed them only superficially.—
>
> Fosberg (1949)

F. Raymond Fosberg, one of the leading atoll scientists of the 20th century, commented early on that the ecological communities on atoll islets are commonly yet falsely regarded as uniform (Fosberg, 1949). However, before beta-diversity was formalized, observations on the compositional dissimilarity of an atoll's islets could not be generalized beyond eloquent descriptions. Here, we provide the first quantification of beta-diversity between the islets within atolls on a global scale. We show that both components of beta-diversity, within-atoll (i.e., between the islets of an atoll) species turnover and nestedness, are common features in vascular plant, reptile, and bird atoll communities. The degree of within-atoll species turnover increases with the number of tropical cyclones that frequent an atoll. Atolls that are more frequented by tropical cyclones show higher species turnover between their islets, likely because of repeated local extinction and re-colonization processes over time and the strong priority effects and historical contingency brought about by such recurring catastrophic disturbance events (Fukami, 2015; Spiller et al., 1998; Stoddart & Walsh, 1992).

The detected increase in within-atoll species turnover under increasing cyclone frequencies suggests that the predominant effect of tropical cyclones for atoll terrestrial community structure is non-homogenizing. Damage caused by tropical cyclones comprises defoliation and topping over of the vegetation, inundation, salinization of the groundwater, scraping-off of the topsoil layers, coastal erosion, and deposition of new sand and coral rubble material onto existing islets (Wiens, 1961). Despite the small spatial extent of atolls (average spatial dimensions of atolls ca. 50 × 30 km), these destructive effects of a tropical cyclone are usually confined to only a subset of their islets each time, generally those on the windward side of the cyclone track and having an island morphology more susceptible to erosion (Duvat et al., 2021; Stoddart, 1963). Therefore, the likelihood of an atoll species becoming locally extinct (extirpated) as a result of a passing cyclone is contingent on the position of the islet within an atoll relative to the cyclone track. This means that a cyclone is not impacting the entire atoll landscape, but only causing local extinction of terrestrial species on some of the islets of an atoll, which varies between each cyclone depending on its exact trajectory across the atoll (Bayliss-Smith, 1988; Blumenstock, 1958). Different species of

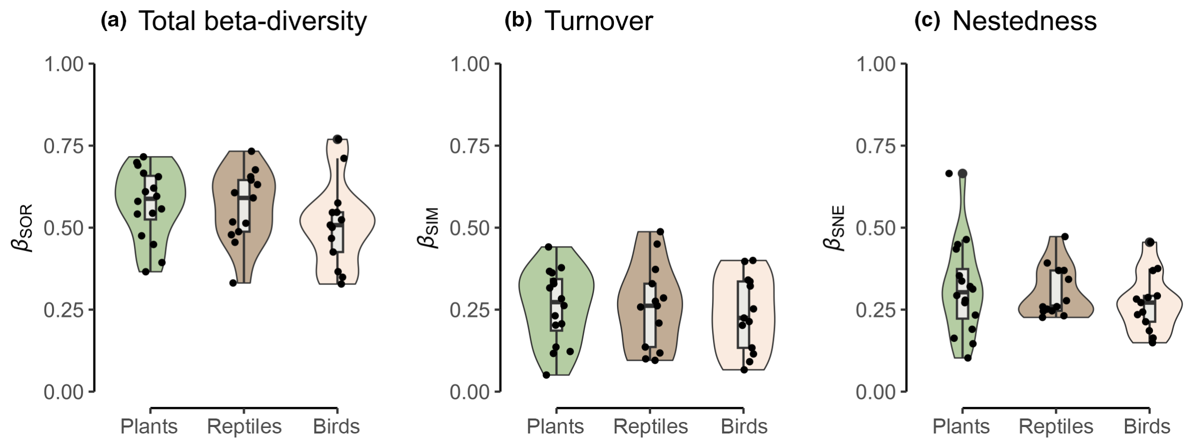

FIGURE 2 Within-atoll beta-diversity (a), species turnover (b), and nestedness (c) on atolls. Each data point represents the multiple-site beta-diversity metric across the islets within one atoll. β_{SIM}, β_{SOR}, and β_{NES} are bound between 0 and 1, with higher values indicating higher total beta-diversity, turnover, and nestedness, respectively.

TABLE 1 Comparison of within-atoll and between-atoll species turnover.

Species group	Within-atoll turnover β_{SIM}	Between-atoll turnover β_{SIM}
Plants	0.256 ± 0.112	0.564 ± 0.166
Reptiles	0.260 ± 0.128	0.298 ± 0.167
Birds	0.238 ± 0.115	0.267 ± 0.160

Note: Within-atoll turnover is the average (mean ± SD) compositional species turnover across the individual islets within each atoll. Between-atoll turnover is the average (mean ± SD) pairwise compositional species turnover between the 29 investigated atolls, combining the islet-wise species occurrences per atoll.

plants, birds, and reptiles on atolls also respond markedly differently to the environmental stress caused by saltwater, wind, or sediment re-working, resulting in asymmetric local population declines and extinctions (Fosberg, 1961; McCoid, 1996; Schoener et al., 2004). Furthermore, depending on the islet's location within the atoll relative to the cyclone track and the predominant current and wind directions, anything from predominantly fine sand to coarse rubble sediments are deposited (Duvat et al., 2020). The type of deposited material affects the vegetation recovery and succession, as certain plant species are better adapted to re-colonize either coarse coral rubble or fine sand deposits, which further adds to the contingency of the cyclone impact and subsequent re-colonization and regeneration patterns (Lee, 1984). In sum, the different islets of the atoll thus initiate their ecological recovery and succession trajectory under different post-cyclone environmental conditions and filters and with a different survivor community (Schoener & Spiller, 2006). These elements combined likely drive the here-documented compositional turnover between islet communities within atolls under increasing cyclone frequency. Regeneration and succession of atoll floras back to climax species community can take 60–100 years after a major disturbance event (Stoddart, 1964). Therefore, those atolls with tropical cyclones passing more frequently (e.g., Sorol or Ulithi

TABLE 2 Effect sizes on species turnover of atolls.

Fixed effect	Estimate	95% CI	*p*-value
Tropical cyclone frequency			
Plants	0.058	[0.002, 0.132]	0.022*
Reptiles	0.075	[−0.046, 0.257]	0.027*
Birds	0.075	[−0.044, 0.247]	0.016*
Total atoll land area			
Plants	0.017	[−0.026, 0.077]	0.254
Reptiles	0.009	[−0.083, 0.172]	0.408
Birds	0.031	[−0.067, 0.187]	0.197
Number of islets			
Plants	0.004	[−0.036, 0.058]	0.449
Reptiles	0.009	[−0.081, 0.162]	0.412
Birds	0.023	[−0.077, 0.185]	0.296
Distance to nearest landmass			
Plants	0.004	[−0.045, 0.077]	0.454
Reptiles	0.031	[−0.076, 0.210]	0.164
Birds	0.019	[−0.081, 0.195]	0.268

Note: Note that slope estimates are based on standardized covariates, so they correspond to a change of 1 standard deviation of the fixed effects. *p*-values are based on the posterior predictive distributions.
*$p < 0.05$.

Atoll, Micronesia, with one tropical cyclone per decade on average) experience local extinctions and habitat heterogenization more frequently, resulting in higher compositional dissimilarity and species turnover rates within atolls that lay inside the tropical cyclone belts.

The effects of tropical cyclone frequency on bird species turnover, which are predominantly seabirds on atolls, are most likely not the result of direct mortality and local extinctions, but rather due to the changes in habitat composition and heterogeneity. The different seabird species commonly found on atolls use different micro-habitats within the atoll landscape, like certain tree or shrub

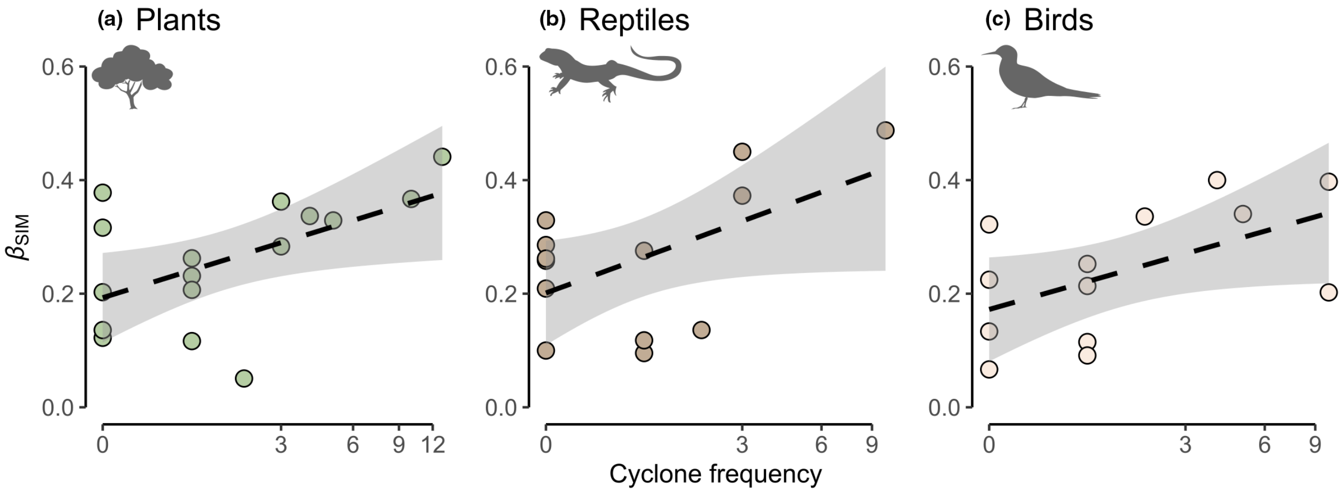

FIGURE 3 Effect of cyclone frequency on the within-atoll species turnover. Species turnover increases for plants (a), reptiles (b), and birds (c) with higher cyclone frequency. Each data point is the multiple-site species turnover measure (β_{SIM}) for one atoll.

species, for nesting (Reynolds et al., 2015). Where catastrophic disturbances alter these breeding grounds (e.g., by the destruction of the coastal fringing vegetation belt, or open grassland areas), large seabird colonies can become displaced from an islet altogether (Schreiber & Schreiber, 1984). Besides disturbances, seabird colonies within atolls are never randomly distributed but usually found in sectors of the atoll, where seabirds can access open ocean fishing grounds rapidly and in multiple directions (Kepler et al., 1994). This likely further adds to the observed beta-diversity and species turnover in atoll seabird communities between the islets within atolls, beyond disturbance-related drivers.

Similarly, natural environmental gradients across an atoll landscape are potentially further contributing to within-atoll community dissimilarity in vascular plant assemblages (Lee, 1984). Atolls have pronounced wind- and leeward sides determined by prevailing wind and oceanic current directions. These oceanic forces control sediment composition, exposure to salinity, and other biophysical gradients on the different islets within an atoll. These persistent natural gradients, in turn, control assembly of plant species with different edaphic prerequisites or salinity tolerances on the different islets within an atoll and likely further contribute to compositional turnover within atolls, beyond any disturbance effects (Fosberg, 1953). This assembly mosaic of plant communities within the atoll landscape is likely also contributing to compositional turnover in atoll faunas, such as reptiles, where different species prefer either open or densely forested patches (McCoid, 1996).

Conceptually, beta-diversity, that is, the compositional dissimilarity of ecological communities among sites, can arise due to stochastic processes in colonization, dispersal, and local extinction of a given community (the neutrality hypothesis) (Hubbell, 2005), or due to heterogeneity in environmental factors that determine the presence or absence of species across a landscape (the niche-assembly hypothesis) (Hutchinson, 1978). As predicted by MacArthur and Wilson's model of island biogeography, the species communities on the remote, small, and low-lying islets of atolls are particularly prone to extinction (MacArthur & Wilson, 1967), and the destructive power of tropical cyclones are likely among the key causes behind local extinction events on atoll (Stoddart & Walsh, 1992). Rather than having uniform impacts across the islets within an atoll, cyclone impacts are restricted to only a subset of islets at any time (Stoddart, 1971), and thus promote strong priority effects and historical contingency between the different islets within an atoll.

Generally, the ecology and geomorphology of atolls are tightly linked to recurring catastrophic disturbances from tropical cyclones, for example, for sediment accretion, seedling dispersal, and for facilitating vegetation succession (Bayliss-Smith, 1988; Duvat et al., 2020; Kench et al., 2018). The results of our analysis indicate that tropical cyclones are also likely drivers for the compositional turnover observed on the different islets within an atoll, thereby facilitating a heterogeneous distribution and compositional dissimilarity within the atoll landscape. While the frequency of tropical cyclone passing had no significant effect on the within-atoll nestedness component of beta-diversity, our analysis demonstrated that nestedness (i.e., differences in species richness between sites) is a common property of atoll terrestrial communities, likely because the different islets of an atoll can be considered analogous to habitat fragments of different sizes and quality, which drives differences in species richness (Morrison, 2013). At the same time, the 'classic' biogeographic parameters appeared to have no significant directional effect on within-atoll turnover and nestedness, in line with earlier notions that atoll terrestrial communities are predominantly controlled by ecological factors and periodic disturbances (Stoddart & Walsh, 1992).

In recent years, atolls have been receiving a growing attention from conservation and restoration science. The individual islets of atolls have repeatedly been considered as ecosystem replicates to compare the effects of different anthropogenic impacts or management actions (e.g., Graham et al., 2018; Steibl et al., 2022). The results of our global analysis of atoll beta-diversity caution against treating the different islets within an atoll as replicated ecosystems, as we show that species turnover occurs naturally between the different islets of an atoll, which might not necessarily be the product of a human impact or conservation intervention.

Beyond these methodical considerations for ecosystem studies and conservation science on atolls, the documented beta-diversity patterns of atoll communities also have relevance for ecological restoration. Beta-diversity is generally considered a resilience trait of ecosystems, as local extinctions can be compensated rapidly by re-colonization of functionally similar or equivalent species from within the metacommunity (Mori et al., 2018). Land management on atolls may thus consider maintaining or facilitating these natural assemblage heterogeneities on the different islets as a potential resilience factor of the atoll meta-community by designating multiple islets of an atoll as protected sites.

The assembly and diversity of ecological communities on islands has always been an intensively researched area in ecology and biogeography (Ricklefs, 1987). Because mostly focused on topographically complex and species-rich archipelagos, little information exists about the controlling factors for terrestrial species assembly on coral atolls. Despite, or, in fact, *due to* their small land areas, low elevation, and thus proneness to localized extinctions from catastrophic disturbances, we show that compositional heterogeneity within atolls is a common biogeographic pattern, rendering the individual islets that comprise an atoll a mosaic of individual community assemblages, continuously a-synchronized by tropical cyclones.

AUTHOR CONTRIBUTIONS

Sebastian Steibl designed the study, compiled the dataset, and analysed the data. Sebastian Steibl and James C. Russell both wrote the manuscript and approved the final version of the manuscript for submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicting interests.

DATA AVAILABILITY STATEMENT

All raw data and statistical code are openly available in Figshare at https://doi.org/10.17608/k6.auckland.24002277.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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