RESEARCH ARTICLE

Effect of topographic complexity on species richness in the Galápagos Islands

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Abstract

Aim: The accumulation of species through time has been proposed to have a hump-shaped relationship on volcanic islands (highest species richness during intermediate stages of an island's lifespan). Change in topographic complexity (TC) of islands over time is assumed to follow the same relationship. However, TC can be measured in different ways and may not have the same impact across taxonomic groups. Here, we quantify TC across the Galápagos Islands and test the assumption that TC follows a predictable trajectory with island age. Subsequently, we ask whether including TC improves statistical models seeking to explain variation in species richness across islands.

Location: Galápagos Archipelago, Ecuador.

Taxon: Native and endemic terrestrial animals and plants.

Methods: For each island, we generated eight TC indices from a 30-m resolution digital elevation model. We tested for a relationship between each index and island age, and whether it significantly contributes to observed variation in species richness, using 11 different models for 12 taxonomic groups across the Galápagos Islands.

Results: Four TC indices were significantly negatively correlated with either island age or ontogenetic age and only one index followed the hump-shaped relationship with age. No index consistently contributed to the variation in species richness for all taxonomic groups. However, for all 12 taxonomic groups, incorporating at least one TC index in modelling species richness improved one or more models. The most common TC index improving models was standard deviation of slope, although each index improved at least five models across all taxa. Different factors predicted taxon-specific richness, and habitat diversity was significant for all taxa.

Main conclusions: Topographic complexity is an important component influencing species richness, but its impact likely differs among taxonomic groups and different scales. Therefore, future studies should incorporate broad, multi-dimensional measures of TC to understand the biological importance of TC.

KEYWORDS
biodiversity, colonization, general dynamic model, habitat diversity, island biogeography, island endemism, island ontogeny, overwater dispersal, topography, volcanic islands

1 | INTRODUCTION

Environmental heterogeneity (EH), an expansive measure of ecosystem complexity including a variety of biotic and abiotic components of a landscape, has been routinely linked to increased biodiversity across habitats on a global scale (Stein et al., 2014; Stein & Kreft, 2015). One component of EH, topographic complexity (TC, the heterogeneous property of terrain components across a landscape), also influences biological diversity across a range of ecosystems and taxonomic groups (e.g. habitat diversity in montane regions [Badgley et al., 2017; Rahbek, Borregaard, Antonelli, et al., 2019; Rahbek, Borregaard, Colwell, et al., 2019]; fish assemblages around coral reefs [Friedlandera & Parrishab, 1998]; plant species richness in California [Richerson & Lum, 1980]; bird species richness in Western Hemisphere [Ruggiero & Hawkins, 2008] and mammal diversity in Australia [Williams et al., 2002]). However, the importance of TC in determining species richness relative to other factors (e.g. area and isolation) is less understood.

Species differ in their interactions with a landscape, and the components of TC in heterogeneous landscapes that have been used reflect these differences (Yu et al., 2015). Common indices used to evaluate TC include elevation, slope (rate of elevational change over the horizontal surface), curvature (rate of slope change over the surface) and aspect (azimuth direction of slope). These topographical components of a landscape affect organisms by shaping local water and energy budgets in different ways (Peterman & Semlitsch, 2013). Elevation has been used as a proxy for environmental factors, such as air temperature, atmospheric pressure and wind speed. Slope and curvature affect water movement, soil erosion and water and soil accumulation (Gosz & Sharpe, 1989). Aspect influences the amount of solar light that a location will receive. Because organisms use the landscape in different ways, the manner in which scientists measure TC is often study- and taxon-specific. While these studies provide intrinsic benefit to illuminating a given species' ecology, this specificity hinders broader application across biogeographic systems and taxonomic groups.

The quantification of TC is highly tractable on volcanic islands since geologic timelines are relatively recent and often diagnosable with some accuracy (Borregaard et al., 2017). Therefore, quantifying the relationship between ontogeny and biodiversity of volcanic islands is attainable because the stages of the geological formation are remarkably predictable. In brief, a volcanic island gains in size and height quickly after emerging above water, reaching maximum area and elevation at the peak of volcanic activity early in an island's lifespan (Jackson, 2013). Subsequently, through a much slower process, islands erode and subside until the landmass is completely submerged (Valente et al., 2014). During the erosion process, some areas of the island erode faster than others, resulting in uneven surfaces, which increase landscape complexity. Thus, over the island's ontogeny, TC is expected to first increase and then eventually decrease (Borregaard et al., 2016;

Whittaker et al., 2008). This hump-shaped relationship representing a change in TC over time has been assumed to be a determinant in the accumulation of biological diversity on islands (Stuessy, 2007; Whittaker et al., 2008).

Several models linking island ontogeny and biodiversity have been proposed (e.g. Heaney, 2000; Paulay, 1994; Stuessy, 2007; Whittaker et al., 2008), wherein each island in an archipelago is used as a snapshot in time. The variation in biodiversity across islands of different ages presumably reflects changes in biogeographical features that have occurred over time (e.g. area and isolation). Since habitats change over time (due to changes in abiotic and biotic factors), the richness and assemblage of species present on islands will likewise change. The general dynamic model (GDM) of oceanic island biogeography proposes that each island has an environmentally determined carrying capacity associated with age, resulting from changes over time in the island's area, TC and habitat diversity (Carey et al., 2020; Whittaker et al., 2008). Richness of native and endemic species should follow a hump-shaped relationship over time with the greatest number of species found at intermediate stages when the island reaches its presumed maximum carrying capacity. This pattern is expected because an island's carrying capacity should peak when the landscape is the most topographically complex, creating the most opportunities for within-island allopatric speciation (Whittaker et al., 2008). Barajas-Barbosa et al. (2020) found EH to be the main driver of plant diversity in volcanic archipelagoes by analysing 20 different metrics of EH in both native and single-island endemic species. They also found strong support for EH to follow a hump-shaped relationship with island age, in concordance with predictions by the GDM.

Similar to EH, TC should be highest shortly after the maximum area and elevation are reached, and then slowly decline over time due to erosion (Nunn, 1994; Whittaker & Fernandez-Palacios, 2007). Due to the heterogeneous nature of many landscapes and the diversity of organisms inhabiting them, a single index of TC may fail to capture the complete range of landscape dynamics affecting island diversity across taxonomic groups, so using a range of TC indices is necessary to capture changes in topography. Dispersal modes may also affect how species interact with the landscape, exemplified in taxa that have successfully colonized oceanic archipelagoes (e.g. Fajardo et al., 2019). Species with limited dispersal abilities may be more impacted by small changes in topography than species with greater dispersal abilities.

Here we use the Galápagos Archipelago to test whether variation in TC influences species richness across islands at different stages of ontogeny and whether this influence is taxon-dependent. While most studies only employ one or two measures of TC when examining biodiversity, here we use eight TC indices and 12 taxonomic groups (terrestrial plants and animals) to address three questions: (1) does TC vary predictably across island ontogeny, (2) does TC contribute to the variation in species richness observed across islands and (3) does that contribution vary across taxonomic groups.

2 | MATERIALS AND METHODS

2.1 | Island species richness

We obtained distribution data for terrestrial native and endemic species of the Galápagos Islands from the Charles Darwin Foundation Datazone (CDFD; Bungartz et al., 2009) (Table S1.1). We tested models explaining variation in total number of native and endemic species across the islands for the following taxonomic groups: plants (vascular plants and bryophytes), invertebrates, mammals, non-avian reptiles (hereafter simply 'reptiles') and birds. We also included additional categories, treating all vertebrates and all animals as single units. Models were validated by visual inspection of the residuals as plotted in R. Our analyses tested the influence of TC on species richness across the terrestrial landscape, so we excluded animals that regularly utilize marine habitats (seabirds and marine mammals/reptiles). Two metrics of species richness were used: numbers of native and endemic species (N + E) and single island endemics (SIE; i.e. endemic to one island). SIE can be a measure of within-island speciation or contribution of in situ evolution to species richness (Peck et al., 1999; Whittaker et al., 2010). For mammals, reptiles and birds, SIE was not analysed due to the small sample sizes which resulted in several of the islands not having a single SIE. Additional analyses used a data set of SIE terrestrial snails (limited to the genus *Naesiotus*), comprising a single endemic adaptive radiation (Parent & Crespi, 2006; Phillips et al., 2020) for which higher spatial resolution range maps are available (Table S1.2). The differences between the data sets are that the snail data set: (1) includes the island of Rábida and (2) Isabela Island is split into the six individual volcanoes forming this island, which arose independent of one another (Geist, 1996). Isabela is the only island subdivided in our study due to clear boundaries between the volcanoes formed by lava fields which are significant dispersal barriers to terrestrial

fauna. We also excluded Darwin and Wolf Islands from our study because these islands are outside the geographical extent of the available maps needed to compute TC.

To sum, in addition to the snail data set, we assembled 11 species richness data sets from CDFD: N + E plants (NE_P), SIE plants (SIE_P), N + E animals (NE_A), SIE animals (SIE_A), N + E vertebrates (NE_V), SIE vertebrates (SIE_V), N + E mammals (NE_M), N + E reptiles (NE_R), N + E birds (NE_B), N + E invertebrates (NE_I) and SIE invertebrates (SIE_I).

2.2 | Island area, isolation, age and habitat diversity

For each island and volcano forming Isabela, we computed island area, isolation and age. ArcMap 10.3.1 (Esri, 2014) was used to establish the boundaries between volcanoes on Isabela as the lowest elevation of the lava fields separating volcanoes. Island area was calculated by using the zonal statistics tool in ArcMap. Isolation was calculated by averaging the shortest pairwise distances (coast-to-coast) from each focal island to every other island. Ages were obtained from Geist et al. (2014) and ontogenetic ages (calculated as the percentage of an island's lifespan) were obtained from Kraemer et al. (pers. comm.).

Habitat diversity was expressed as the number of habitat types found on each island as defined by the Terra and Aqua Combined Moderate Resolution Imaging Spectroradiometer (MODIS) Version 6 global Land Cover data (MCD12Q1) with a spatial resolution of 500 m for the year 2018 (Friedl & Sulla-Menashe, 2019). The data were acquired from NASA EarthData and are a product of the Land Processes Distributed Active Archive Center (LP DAAC). Land cover is divided into 17 classes using the Annual International Geosphere-Biosphere Programme (IGBP) classification. Ten of the land cover classes were observed in the Galápagos Archipelago (Figure 1). The land cover class names have been changed from the IGBP to reflect
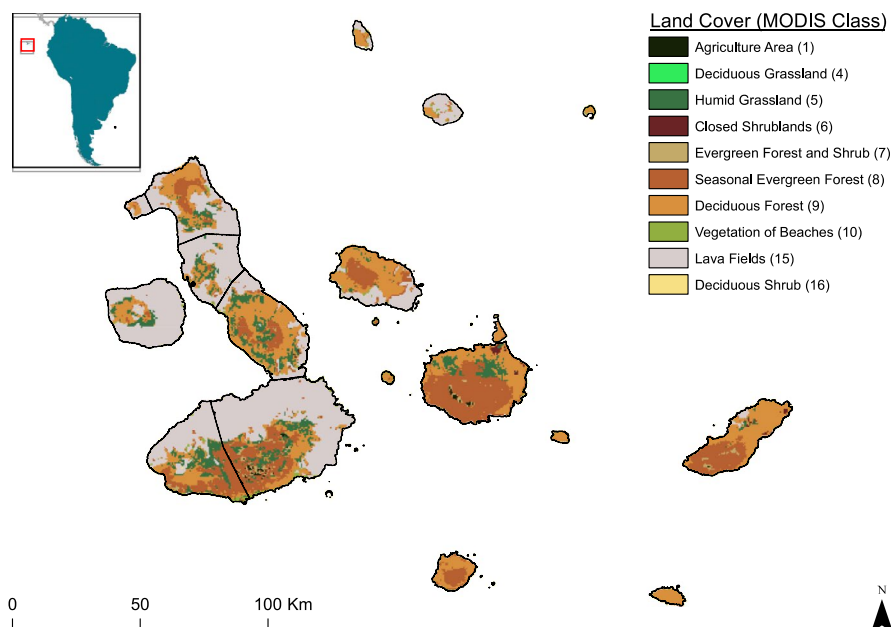
FIGURE 1 MODIS land cover classes across the Galápagos Islands with names adapted to local conditions. The inset map shows the location of Galápagos relative to South America

Land Cover (MODIS Class)
- Agriculture Area (1)
- Deciduous Grassland (4)
- Humid Grassland (5)
- Closed Shrublands (6)
- Evergreen Forest and Shrub (7)
- Seasonal Evergreen Forest (8)
- Deciduous Forest (9)
- Vegetation of Beaches (10)
- Lava Fields (15)
- Deciduous Shrub (16)

0   50   100 Km

the local land cover type. MODIS data have been used in previous studies to generate a variety of habitat indices (Radeloff et al., 2019; Tuanmu & Jetz, 2015).
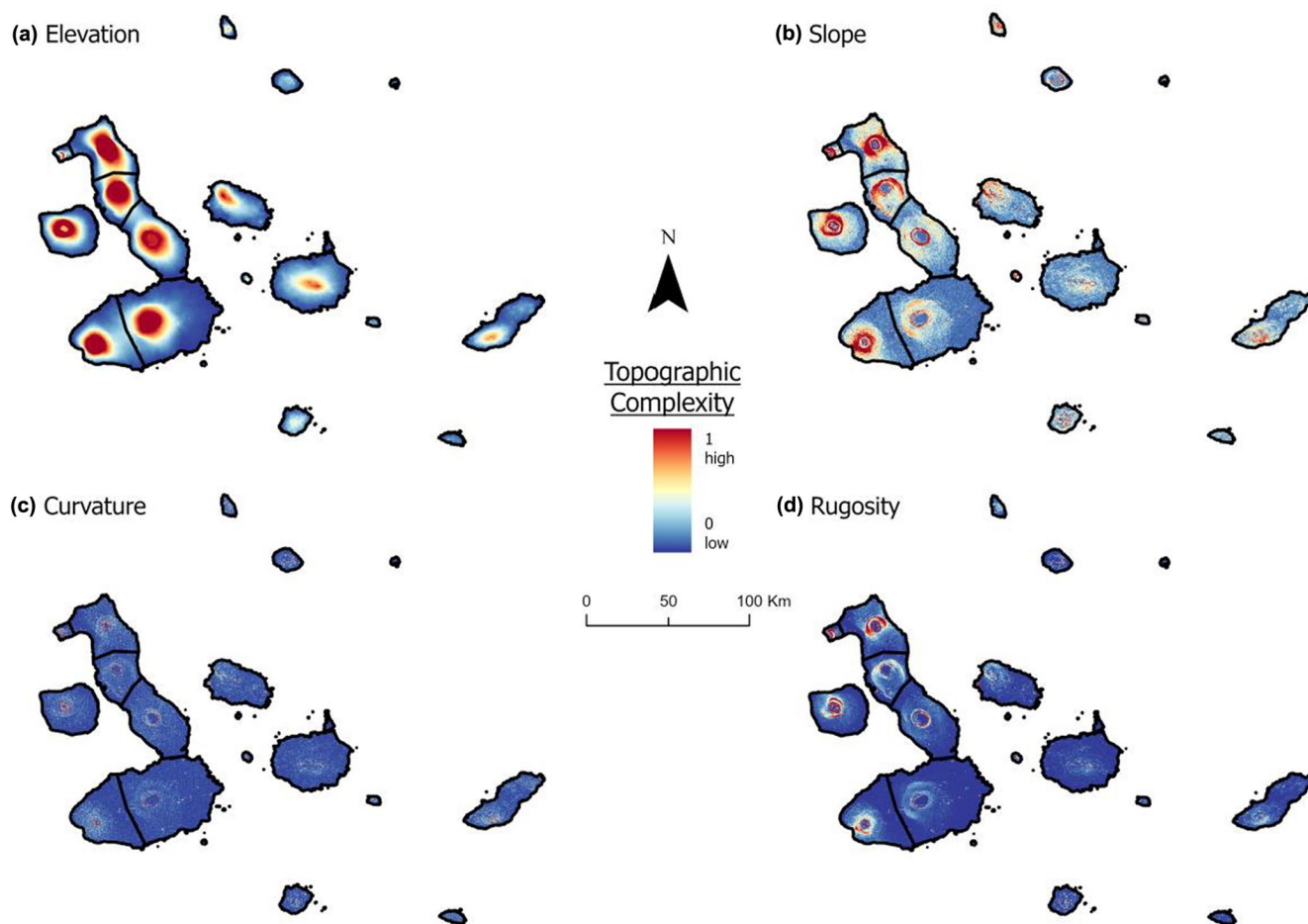
2.3 | Island topographic complexity

We calculated topographic complexity (TC) indices based on a 30-m resolution digital elevation model (DEM) downloaded from USGS Global Data Explorer using the NASA Shuttle Radar Topography Mission 1 arc-sec data (NASA, 2013). We created three rasters from the DEM (Figure 2, rasters in supplementary): slope (using the Spatial Analyst Toolbox from ArcMap), curvature, and rugosity (the last two using the DEM Surface Tools extension from Jennessent [Jenness, 2013]). We computed eight topographic indices: range and standard deviation of elevation (RE and SE, respectively), range and standard deviation of slope (RS and SS, respectively), total and standard deviation of curvature (CU and SC, respectively), rugosity (RU) and compound terrain complexity index (CTCI; Lu et al., 2007). CTCI uses four indices (RE, SE, CU and RU) to generalize the landscape (Lu et al., 2007). Each index was calculated per island using the zonal

statistic tool in ArcMap. TC indices for all islands and volcanoes are reported in Table S1.3. We hypothesize that species richness in all groups will increase with each of these indices, as higher values indicate more complex landscapes.

2.4 | Statistical analyses

To test the relationship between age and topographic complexity (TC) hypothesized by Whittaker et al. (2008), we also assessed the relationship between island age across the Galápagos and TC, independently testing each TC index. We used the island age to determine if there is either a linear or quadratic relationship with TC. Testing a quadratic formula (Time + Time^2) represents the hump-shaped relationship described in Whittaker et al. (2008). Since our metric for ontogenetic age is a percentage, it was not appropriate for use in Time + Time^2 and thus only geologic age was used for this model. The models to test the relationship between island age and TC were generalized linear models.

To predict species richness across the archipelago in both native and endemic (N + E) and single-island endemic (SIE) species,

FIGURE 2 Rasters used to compute indices of topographic complexity for Galápagos. Isabela Island is divided into six separate areas by volcano for the snail data set. Because distribution data are not available at the volcano level for the Charles Darwin Foundation Datazone, Isabela is considered as a single island for these data sets

TABLE 1 Models tested as predictors for species richness in different taxonomic groups in the Galápagos Archipelago

Models
Time
Time^2
Time$_o$
Log (Area)
Isolation
Habitat Diversity
Time + Time^2
ATT^2
ATT^2 + Isolation
ATT^2 + Isolation + Habitat Diversity
TC (eight different indices)

Note: Time is geologic age and Time$_o$ is ontogenetic age.
Abbreviations: ATT^2, Log(Area) + Time + Time^2, where Time is equivalent to geologic age; TC, Topographic complexity index.

TABLE 2 *p*-values indicating if island age is a significant predictor of topographic complexity (TC) indices

TC index	Time	Time + Time^2	Time$_o$
RE	**0.032 (0.21, −)**	0.077	**<0.001 (0.84, −)**
SE	**0.019 (0.25, −)**	**0.047 (0.25, −, +)**	**< 0.001 (0.86, −)**
RS	0.116	0.260	**0.002 (0.42, −)**
SS	0.492	0.759	0.631
CU	0.754	0.951	0.977
SC	0.954	0.922	0.586
RU	0.876	0.514	0.664
CTCI	**0.019 (0.26, −)**	0.058	**<0.001 (0.82, −)**

Note: Bolded values are *p*-values <0.05, followed by R^2 and the direction of this relationship (positive or negative via the island age coefficient from the model) in parentheses. For Time + Time^2, Time has a negative effect, whereas Time^2 has a positive effect for the SE model.
Abbreviations: CTCI, Compound terrain complexity index. Time, Geologic age; CU, Total curvature; RE, Range of elevation; RS, Range of slope; RU, Rugosity; SC, Standard deviation of curvature; SE, Standard deviation of elevation; SS, Standard deviation of slope; TC Index - Time, Geologic age; Time$_o$, Ontogenetic age.

we built models to test for a relationship with species richness in each of the 12 taxonomic data sets. Each data set was used to test a series of 11 models to explain variation in species richness across islands (Table 1). These models included island age (time), area, isolation, habitat diversity, ATT^2 (Log(Area) + Time + Time^2) and combinations therein. We additionally tested models that used each TC as the sole variable to determine if TC alone explains species richness. We used a negative binomial distribution with a log link function in all our model testing given that our response variable (species richness) is represented by over-dispersed count data. Every one of these models was tested independently and had no impact on the results of one another.

TC indices were standardized before being incorporated in models to allow comparisons among different indices. In order to reduce the total number of models tested in this study and given that our aim is to test whether the inclusion of TC would improve the fit of models, such as the GDM, TC indices were only added to models that were already significant when explaining species richness (p < 0.05). All eight indices were tested independently (due to multicollinearity among some indices, Table S1.6). If the Akaike Information Criterion (AIC) decreased with the addition of a TC index, we considered the model as improved. Coefficient estimates of TC indices were recorded to determine the effect that TC has on species richness. All statistical analyses were performed in R.

3 | RESULTS

Using the broader set of 18 islands (including Isabela's volcanoes as separate islands), both geologic and ontogenetic age were significant predictors of range of elevation (RE), standard deviation of elevation (SE) and compound terrain complexity index (CTCI; Table 2). Ontogenetic age was also a significant predictor of RS. Geologic and ontogenetic age had a negative relationship with topographic complexity (TC) indices for all significant models (p < 0.05). Variation in SE was significantly explained with a quadratic function (Time + Time^2), representing the predicted hump-shaped relationship between one measure of TC and island age (Whittaker et al., 2008).

No TC index consistently improved models for all taxonomic groups and no single model was the best fit across all plant and animal data sets. However, for every data set, the model with only habitat diversity was always significant. The number of models that were significant for taxonomic groups ranged from 2 to 7 out of the 12 tested (Figure 3, Table S1.4). Of the 58 significant models that explained species richness without a TC index, 29 were improved with the addition of a TC index (50%). The most common TC index that improved models was SS (18 of 29 improved models). The effect TC indices had on models, either having a positive or negative relationship, varied depending on the taxonomic group, except SS always had a negative effect on species richness (Figure 4, Table S1.5). The difference in Akaike Information Criterion (AIC) from models with no TC index and improved models with a TC index ranged from 0.1 to 8.2 with an average of 2.0 (Tables S1.4–S1.5). The species richness for five of the taxonomic groups was also significantly explained with a TC index alone. Incorporating a TC index in modelling species richness benefited at least one model in all taxonomic groups (Figure 3). The complete list of results for significant models is reported in Table S1.4. Below we detail the results and indicate the best model (lowest AIC) for each taxonomic group.

3.1 | Plants

The variation in native and endemic plants (NE_P) was best explained by ATT^2 + Isolation but was also significant for ATT^2, ATT^2 + Isolation
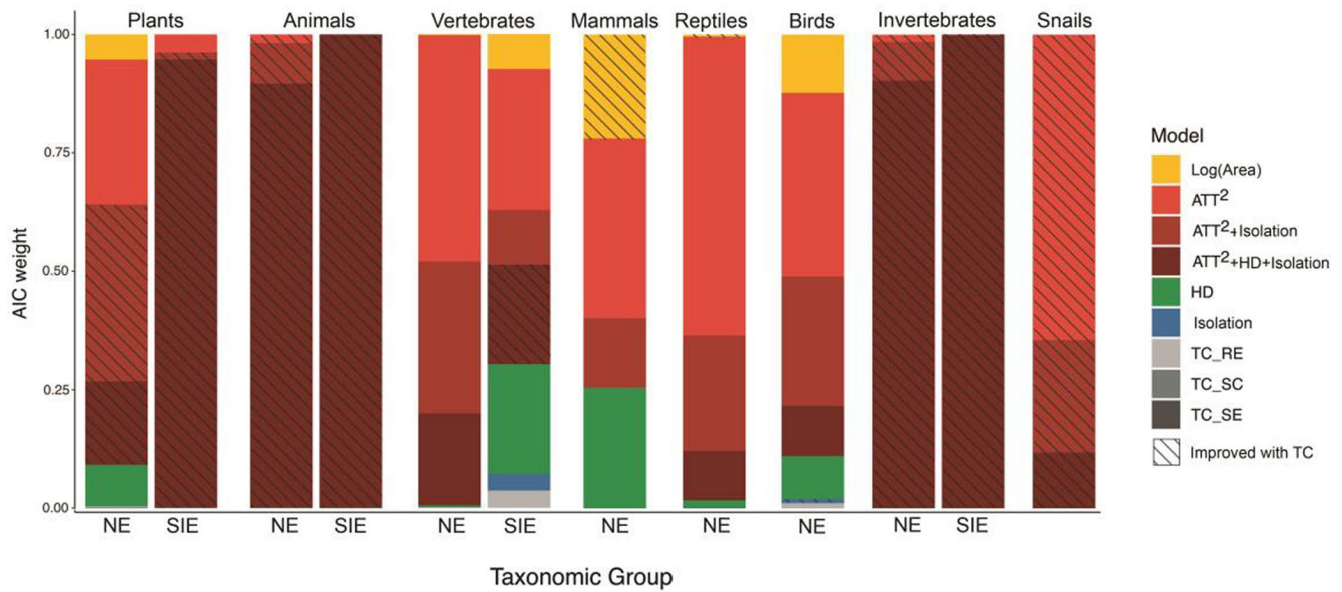
FIGURE 3 Model support for predictors of species richness in Galápagos taxa. Akaike Information Criterion (AIC) weights display the relative support for only the significant candidate models ($p < 0.05$). Models improved by adding an index of topographic complexity (TC) are denoted by cross-hatching. AIC values for all significant models can be found in Table S1.4. ATT^2, Log(Area) + Time + Time^2; HD, Habitat diversity; NE, Native and endemic species; RE, Range of elevation; SC, Standard deviation of curvature; SE, Standard deviation of elevation; SIE, Single Island Endemic species

+ Habitat Diversity, habitat diversity, area and the topographic complexity (TC) indices for RE and standard deviation of elevation (SE). The independent addition of seven TC indices (all except standard deviation of slope; SS) improved two of the models. Variation in SIE_P across the archipelago was best explained by ATT^2 + Isolation + Habitat Diversity and was also significant for five other models. Four of the six models were improved by at least two TC indices.

3.2 | Animals

ATT^2 + Isolation + Habitat Diversity was the best model for explaining species richness for both native and endemic animals (NE_A) and single-island endemic animals (SIE_A). For NE_A, five models were significant, all of which were improved by adding a topographic complexity (TC) index. For SIE_A, the best model (ATT^2 + Isolation + Habitat Diversity) was improved with the addition of two TC indices (range and standard deviation of slope: RS and SS, respectively). These results may have been strongly influenced by the inclusion of invertebrates in the data set (around 90% of the data set for each island), yet NE_A and native and endemic invertebrates (NE_I) still differed in one model. The TC index standard deviation of curvature (SC) was significant for NE_I, but not NE_A.
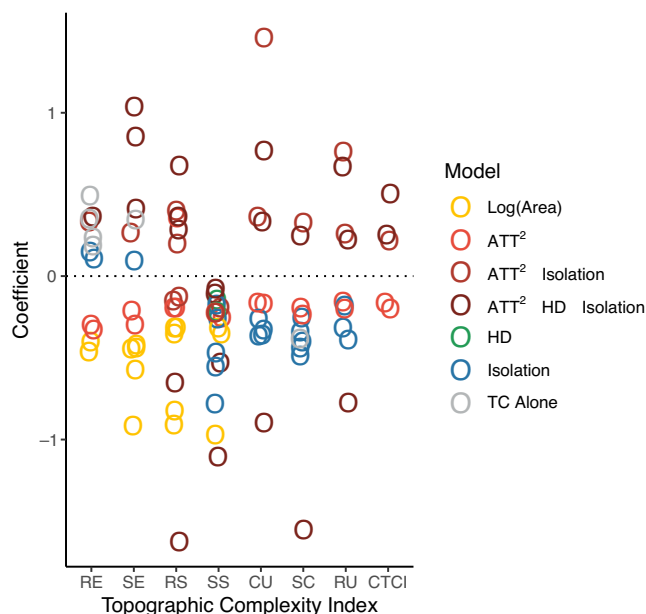
3.3 | Vertebrates

The variation in both native and endemic vertebrates (NE_V) and single-island endemic vertebrates (SIE_V) species richness was

best explained by the hump-shaped curve (ATT^2). Six additional models were significant at explaining the variation in the number of both groups. For NE_V, only the model using island isolation was improved by the addition of topographic complexity (TC) indices ($N = 5$; curvature, range and standard deviations of elevation and slope [CU, RE, RS, SE, SS]) while in SIE_V, both ATT^2 + Isolation + Habitat Diversity and isolation alone improved with the addition of a TC index.

ATT^2 was also the best model for native and endemic mammals (NE_M), native and endemic reptiles (NE_R) and native and endemic birds (NE_B). For NE_M, out of four significant models, only log(area) was improved by adding a TC index (RS and SS). The variation in number of NE_R across the islands was significant for six models, of which two improved with the addition of a TC index. Variation in NE_B richness across the archipelago was significant for seven models, with only isolation improving with the addition of a TC index. Among these seven models, the independent TC index RE was also found to be significant at explaining variation in NE_B.

3.4 | Invertebrates

The variation in both native and endemic invertebrates (NE_I) and single-island endemic invertebrates (SIE_I) was best explained by the ATT^2 + Isolation + Habitat Diversity. Six models were significant for NE_I, one being the independent TC index (standard deviation of curvature, SC) and all others were improved by adding a TC index. Of the two significant models for SIE_I, only ATT^2 + Isolation + Habitat Diversity was improved with the addition of a TC index.

FIGURE 4 Effect of topographic complexity (TC) index when added to significant models for Galápagos taxa. Taxa include 12 taxonomic groups: native and endemic (NE) and single island endemic (SIE) plants, NE and SIE animals, NE and SIE vertebrates, NE mammals, NE reptiles, NE birds, NE and SIE invertebrates and SIE snails. CTCI, Compound terrain complexity index; CU, Total curvature; RE, Range of elevation; RS, Range of slope; RU, Rugosity; SC, Standard deviation of curvature; SE, Standard deviation of elevation; SS, Standard deviation of slope

3.5 | Snails

The variation in snail species richness across the islands was best explained by the model using only ATT^2. A total of five models were significant, four of which were improved by adding a topographic complexity (TC) index.

4 | DISCUSSION

4.1 | Habitat diversity and the GDM

Our results suggest that a combination of island age and ontogeny along with the general dynamic model (GDM) of island biogeography are the most important determinants of species richness in the Galápagos Archipelago. Of the variables tested, habitat diversity had the greatest impact by increasing the explanatory power of the GDM models. This finding underscores the importance of habitat heterogeneity in promoting richness across taxonomic groups (Barajas-Barbosa et al., 2020; Stein et al., 2014; Stein & Kreft, 2015). It is also noteworthy that species richness in fewer taxonomic groups was independently predicted by topographic complexity ($N = 5$) and island isolation ($N = 4$) compared to habitat diversity (all 12 groups).

Species richness for all taxonomic groups in this study was predicted by the GDM (ATT^2 independently for 10 groups and

ATT^2 + Isolation + Habitat Diversity for 11 groups; Table S1.4), even though topographic complexity (TC) itself did not follow the hump-shaped curve as previously predicted. Our findings of ATT^2 as a significant predictor for plants, snails and invertebrates aligns with previous studies (Barajas-Barbosa et al., 2020; Cameron et al., 2013; Cardoso et al., 2010; Steinbauer et al., 2013; Whittaker et al., 2008), and we also find a similar relationship for higher dispersing organisms such as birds. Therefore, our study largely supports that the hump-shaped relationship of island age can predict species richness (Whittaker et al., 2008). However, the degree of association varies by taxonomic group (also see Borges & Hortal, 2009). Notably, our findings reinforce the importance of the GDM, as ATT^2 was the best model for 50% of the groups we tested (the other half still included ATT^2 along with isolation and habitat diversity in their best model; Figure 3, Table S1.4). Our study differs from previous studies in that we fit a linear relationship to the log-transformed expected values, and on the untransformed scale, the relationship may have a very different form. This approach may be similar to the GDM with log-transformed richness (although not with time), although log-transformation of the expected values is not the same as log-transformation of the response. These differences in approach warrant further study in their application to studies of island biodiversity.

4.2 | Topographic complexity

More complex landscapes intuitively contain a greater diversity of ecosystems and therefore have the potential to support a greater number of species. Our analyses suggest that while topographic complexity (TC) is not a universal predictor for species richness in the Galápagos Islands, half of the significant models were improved by including some metric of TC. This enforces the idea that the accumulation of species may increase in topographically complex landscapes (Badgley et al., 2017). Although it has not been explicitly considered in previous models of species richness in islands (e.g. Cabral et al., 2019; Hortal et al., 2009; Lenzner et al., 2017; Weigelt, Steinbauer, Cabral, & Kreft, 2015), TC is assumed to follow a hump-shaped curve with age of the island (Whittaker et al., 2008). Because a common method of measuring complexity is using an RE, volcanic islands (e.g. the Galápagos Archipelago) would demonstrate higher complexity after the volcano has reached a maximum elevation. Allowing for erosion to occur after the maximum elevation has been reached, TC would be the highest during this intermediate age until erosion has caused the peak elevation to significantly decrease. We acknowledge the presence of multicollinearity among several variables (Table S1.6), including established geographic patterns such as habitat diversity increasing on islands with larger sizes and higher elevations (Parent & Crespi, 2006) and expected similarities among TC indices. Two of the TC indices (RE and SE) have a correlation of 0.99, resulting in similar outcomes from the models. Typically, if either RE or SE were significant, the other was as well. However, despite these correlations, no models produced identical results across taxonomic groups, illustrating the taxon-specific patterns in response

to different aspects of TC. Similarly, Barajas-Barbosa et al. (2020) retained different EH variables (e.g. elevation and temperature heterogeneity) that were revealed to be collinear in their analyses to capture different aspects of EH that might have slightly different effects on species richness.

While a single index of TC might capture part of the landscape's complexity, it may similarly fail to assess other important factors that may be important to different taxonomic or functional groups. We find that most TC indices do not follow a hump-shaped relationship with island age for Galápagos Islands. Only one TC index (standard deviation of elevation, SE) exhibited the GDM predicted hump-shaped relationship, whereas geologic and ontogenetic age of the islands were significantly negatively correlated with three and four different indices of TC, respectively.

The inclusion of TC in previous studies improved some models, but findings are typically taxon-specific and do not expand beyond a focal group. Particularly, TC is found to significantly contribute to the variation in plant richness in the Canary Islands, another archipelago of volcanic origin (Irl et al., 2015; Otto et al., 2016). However, both these studies use different definitions of TC making comparisons across studies problematic; Irl et al. (2015) use rugosity, whereas Otto et al. (2016) employ standard deviation of slope. We demonstrate that several metrics for TC are useful in predicting species' distributions, as every measure of TC improved five or more models (Table S1.5). Our findings demonstrate that studies testing how landscape affects species richness should use several TC indices where possible since the effect TC has within models can change depending on the taxonomic group (Table S1.4). Relevant information regarding the formation and maintenance of species richness could be overlooked using one measure of TC.

4.3 | Taxonomic patterns

For all taxonomic groups, incorporating a topographic complexity (TC) index improved one or more models as a predictor of species richness, indicating that finer-scale topographic data sets may reveal important patterns that we were unable to detect (Sears et al., 2011). A lack of statistical significance of TC on improving some models may be due to the coarseness of available digital elevation model (DEM) data which might leave crucial (although, minute) differences in the landscape undetected. Each taxonomic group interacts with the landscape at a specific scale and the scale at which TC is used to predict species richness is thus critical (Yu et al., 2015). This is exemplified in our models as richness for each group of organisms is found to be predicted by a unique set of environmental variables. Habitat diversity was a significant predictor for all groups, while log(area) and all models including ATT^2 were significant for a majority of groups tested (Figure 3). A caveat with models including area and TC indices is that area was correlated with two indices, as well as habitat diversity. For some models, both area and the TC index were significant, suggesting that an independent effect of each variable was contributing to the variation observed. However, for other models,

only one of the two correlated variables was significant. Under such a scenario, it is difficult to evaluate the independent effect of TC, given that area is a crucial component of the general dynamic model (GDM) of oceanic island biogeography.

For species with high dispersal ability (e.g. birds or wind-dispersed plants), fine-scale complexity indices may be irrelevant. Island isolation was significant in models for five taxonomic groups: single-island endemic plants (SIE_P), both vertebrate groups, reptiles and birds. While birds are the most obvious taxa to disperse between islands, lizards are often hypothesized and occasionally observed to disperse to oceanic islands through rafting (Censky et al., 1998; Phillips et al., 2019; Raia et al., 2017), and while Galápagos tortoises are poor swimmers, they can float and survive without food for an extended period of time (Caccone et al., 2002), allowing dispersal to proximate islands. Therefore, the degree of isolation for these groups makes sense as a predictor of species richness while native mammals (mostly from endemic radiation of muroid rats [Schenk & Steppan, 2018]) and low-dispersing invertebrates (including snails, discussed below) may be more impacted by intra-island factors (e.g. area or floral diversity).

Past work on single-island endemic snails and plants in volcanic archipelagoes found richness in both groups to increase with greater area and decrease with isolation (Norder et al., 2019). Our study confirmed the results for these taxa in the Galápagos. Log(area), was significant for all native and endemic (N + E) groups, possibly due to higher rates of colonization of larger landmasses within the archipelago (Cabral et al., 2019; MacArthur & Wilson, 1963, 1967). However, ATT^2 was a better predictor every time in head-to-head comparisons (N = 7, Table S1.4). The effect TC has on species fluctuated in directionality depending on the model. For NE_P, all TC indices added to models had a positive effect while they all had a negative effect for native and endemic animals (NE_A), single-island endemic animals (SIE_A), native and endemic mammals (NE_M) and native and endemic reptiles (NE_R). The effects differed for SIE_P, native and endemic vertebrates (NE_V), single-island endemic vertebrates (SIE_V), native and endemic birds (NE_B) and snails. For plants, we found that the TC indices RE and SE predict species richness in NE_P and improve multiple models in both NE_P and SIE_P. This directly aligns with Barajas-Barbosa et al.'s (2020) findings as four out of five measures of elevation they tested (including RE and SE) increased diversity in both NE and SIE plants (the Galápagos archipelago was included in their data set of 135 volcanic archipelagos).

5 | CONCLUSIONS

In this study, we find that the most consistent predictors of species richness across taxa were habitat diversity and the general dynamic model (GDM) of oceanic island biogeography, with habitat diversity significantly explaining species richness for all taxa. We also tested the assumption that topographic complexity follows a hump-shaped relationship with island age within an archipelago and whether modelling species richness improves when incorporating a topographic

complexity (TC) index. For the Galápagos Archipelago, only one out of eight TC indices considered followed a hump-shaped relationship, and 50% of significant models for predicting species richness were improved by incorporating one TC index. Notably, species richness in native and endemic (N + E) plants, vertebrates, birds, invertebrates and SIE vertebrates was predicted by one or more TC indices alone. This underlines the importance of considering a diversity of topography measures when testing diversity patterns in space. We encourage future workers to consider all of these variables, including topographic complexity when modelling species richness, to assess interactions between species and the landscape. Combined, our findings demonstrate the importance of habitat diversity and topographic complexity in predicting biological patterns and the need to incorporate diverse measures of topography in future studies.

DATA AVAILABILITY STATEMENT
The Charles Darwin Foundation Datazone is publicly available at www.darwinfoundation.org/en/datazone. Due to concerns regarding the conservation status of Galápagos snails, the locality information used in this study is available only directly through the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.