



Species–area relationships on small islands differ among plant growth forms

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Abstract

Aim: We tested whether species–area relationships of small islands differ among plant growth forms and whether this influences the prevalence of the small-island effect (SIE). The SIE states that species richness on small islands is independent of island area or relates to area in a different way compared with larger islands. We investigated whether island isolation affects the limits of the SIE and which environmental factors drive species richness on small islands.

Location: Seven hundred islands (< 100 km²) worldwide belonging to 17 archipelagos.

Major taxa studied: Angiosperms.

Methods: We applied linear and breakpoint species–area models for angiosperm species richness and for herb, shrub and tree species richness per archipelago separately, to test for the existence of SIEs. For archipelagos featuring the SIE, we calculated the island area at which the breakpoints occurred (breakpoint area) and used linear models to test whether the breakpoint areas varied with isolation. We used linear mixed-effect models to discern the effects of seven environmental variables related to island area, isolation and other environmental factors on the species richness of each growth form for islands smaller than the breakpoint area.

Results: For 71% of all archipelagos, we found an SIE for total and herb species richness, and for 59% for shrub species richness and 53% for tree species richness. Shrub and tree species richness showed larger breakpoint areas than total and herb species richness. The breakpoint area was significantly positively affected by the isolation of islands within an archipelago for total and shrub species richness. Species richness on islands within the range of the SIE was differentially affected by environmental factors across growth forms.

Main conclusion: The SIE is a widespread phenomenon that is more complex than generally described. Different functional groups have different environmental requirements that shape their biogeographical patterns and affect species–area and, more generally, richness–environment relationships. The complexity of these patterns cannot be revealed when measuring overall plant species richness.

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KEYWORDS

breakpoint, environmental factors, functional island biogeography, growth form, isolation, plant functional types, small-island effect, species–area relationship

1 | INTRODUCTION

The small-island effect (SIE) describes an “anomalous” feature of species richness on small islands compared with larger ones (Triantis & Sfenthourakis, 2012). Usually, it is defined as the independent variation of species richness with island area on small islands, representing one of the few exceptions to the species–area relationship (SAR; Heatwole & Levins, 1973; Lomolino & Weiser, 2001; but for alternative approaches, see Triantis & Sfenthourakis, 2012). Since its first depiction by Niering (1963), a wealth of studies have reported on the existence of the SIE and put forward several hypotheses to explain it (Lomolino & Weiser, 2001; for review, see Triantis et al., 2006). MacArthur and Wilson (1967) hypothesized that the SIE occurs when species extinctions outnumber colonization events. According to their equilibrium theory of island biogeography, extinction rates are higher on small and isolated islands, whereas larger and less isolated islands have higher immigration rates (Brown & Kodric-Brown, 1977; Lomolino, 1990; MacArthur & Wilson, 1963, 1967). Below a certain island area threshold, and for a given degree of isolation, increasing island area might not affect species richness because extinction rates are still higher than immigration rates, causing an independent variation of species richness with island area (MacArthur & Wilson, 1967). Hence, the SIE prevails on islands where species richness is not governed by a dynamic equilibrium between colonization and extinction events, and the SIE should be more pronounced on more isolated islands that have lower colonization rates than on less isolated islands. Alternative, but not mutually exclusive, explanations for understanding the SIE stress the importance of limited habitat availability (Sfenthourakis & Triantis, 2009; Triantis, Mylonas, Lika, & Vardinoyannis, 2003), the area requirements of species (Schrader, König, Moeljono, Pärtel, & Kreft, 2019), greater influence of disturbances on smaller islands (Whittaker, 1995), alternating effects of niche-based and neutral processes (Chisholm, Fung, Chimalakonda, & O'Dwyer, 2016), or differential effects of isolation, topography and geology (Ackerman, Trejo-Torres, & Crespo-Chuy, 2007; Triantis et al., 2006).

In addition to ecological explanations for the SIE, the importance of analytical and methodological factors has been stressed (Burns, Paul Mchardy, & Pledger, 2009; Dengler, 2010; Gentile & Argano, 2005; Tjørve & Tjørve, 2011). For example, the inclusion or exclusion of empty islands (Dengler, 2010; Wang, Millien, & Ding, 2016; Wang et al., 2015) or the choice of the mathematical model may affect the detection rate of SIEs considerably (Chisholm et al., 2016; Dengler, 2010; Gentile & Argano, 2005; Lomolino, 2000; Matthews, Steinbauer, Tzirkalli, Triantis, & Whittaker, 2014). Overall, the SIE appears to be a common feature of small-island systems worldwide (Chisholm et al., 2016; Wang et al., 2016). However, the wealth of explanations and analytical

considerations behind the SIE indicate that no consensus exists about its underlying processes.

The island area at which the breakpoints of the SIE occur (hereafter referred to as breakpoint area) differs greatly among taxonomic groups. Small or sessile organisms, such as invertebrates or plants, show smaller breakpoint areas than larger or more mobile taxa (Chisholm et al., 2016; Lomolino & Weiser, 2001). Differences between taxa have been attributed to variation in species dispersal abilities, environmental requirements, diet or habitat preferences (Chisholm et al., 2016; Sfenthourakis & Triantis, 2009). However, even within taxonomic groups, dispersal ability and environmental requirements may vary considerably among species (Duckworth, Kent, & Ramsay, 2000; Moles et al., 2005), meaning that it is questionable whether taxonomic groups are useful units to explain differences in the prevalence and breakpoint area of the SIE. In fact, species functional traits may be better predictors of assembly processes on islands (Si et al., 2017), and such a functional island biogeography perspective might provide novel and mechanistic insights into processes shaping the SAR in general (Franzén, Schweiger, & Betzholtz, 2012; Si et al., 2017; Whittaker et al., 2014) and the SIE in particular.

Functional types, such as plant growth forms (herbs, shrubs and trees), are simple but powerful proxies for differences in life-history strategies, dispersal abilities, ecological adaptations and habitat requirements (Knapp et al., 2008; Moles et al., 2005; Wullschlegel et al., 2014), with potential implications for community assembly on islands. Perennial woody species (shrubs and trees), for example, might underlie stronger climatic filtering than annual herbs, due to different strategies to cope with unfavourable conditions (Šimová et al., 2018), such as often occurring on small islands (Schrader, Moeljono, Keppel, & Kreft, 2019; Whittaker, 1995). Herbs often exhibit more diverse ecological adaptations (Pierce et al., 2017) and are, on average, better dispersers than shrubs or trees (Moles et al., 2005; Thomson et al., 2010), suggesting that herbs might reach and establish more frequently on small islands (Abbott & Black, 1980; Panitsa, Tzanoudakis, & Sfenthourakis, 2008). Moreover, herbaceous species can build up larger populations on small islands due to their small size and shorter life cycle (Höner & Greuter, 1988) and might face lower extinction risks compared with larger species. In addition, the distance decay of similarity is considerably shallower for herb assemblages on islands than for shrub or tree assemblages, probably due to the higher dispersal abilities of herbaceous plants (König, Weigelt, & Kreft, 2017). Also, species temporal turnover has been reported to be higher on small islands (Chiarucci et al., 2017; Morrison, 2011) owing to high rates of extinctions and colonizations (MacArthur & Wilson, 1967). Hence, small-island communities should be characterized by dispersive species with fast life cycles, such as herbs (Díaz et al., 2016; Grime, 1977). Trees and shrubs often follow life-history strategies connected to longevity, demographic

stability and resource acquisition (Díaz et al., 2016; Poorter et al., 2008; Westoby, 1998). Consequently, these growth forms are more successful on larger islands, where environmental conditions are more stable and where community assembly is increasingly dominated by competition rather than colonization-extinction dynamics (Chiarucci et al., 2017; Si et al., 2017).

The contrasting strategies of herbs, shrubs and trees, in combination with the different environmental conditions on small and large islands, may have confounding effects on the shape of the SAR (Panitsa, Tzanoudakis, Triantis, & Sfenthourakis, 2006) and, possibly, the breakpoint area of the SIE. Species-area relationships constructed for herbs show steeper slopes compared with SARs constructed for shrubs or trees, which show flatter slopes (Whitehead & Jones, 1969; Woodroffe, 1986). Island isolation might also affect the shape of the SAR differently for different growth forms (Negoita et al., 2016). Moreover, different extinction probabilities might affect the breakpoint area for different growth forms. Larger organisms need larger areas to form stable populations, and their extinction risk increases with decreasing area. Hence, larger organisms might extend the breakpoint area of the SIE to the point where their extinction rates equal colonization events (MacArthur & Wilson, 1967). In their seminal paper on the SIE, Lomolino and Weiser (2001) showed that the shape of the SAR and the breakpoint area of the SIE differ between taxonomic groups (for a discussion of methodological issues of this approach see Dengler, 2010; Gentile & Argano, 2005). Using species richness data from one isolated atoll, Lomolino and Weiser (2001) detected different SIEs for herbs, shrubs and trees, whereas total species richness did not show an SIE. Moreover, Lomolino and Weiser (2001) found the breakpoint area of the SIE to be larger for more isolated islands compared with less isolated ones. However, they provided no specific explanations why the breakpoint area differed between herbs, shrubs and trees and, to our knowledge, no study so far has dissected species richness patterns into different growth forms to test for differential patterns in the shape of the SAR and the prevalence of the SIE for a globally representative dataset.

Here, we contrast SARs for different growth forms and test for the existence of SIEs based on a comprehensive dataset of 17 archipelagos worldwide, featuring a total of 700 small islands and 5,101 plant species. We tested whether the shape of the SAR and the breakpoint area of the SIE differed between herbs, shrubs and trees. We also tested whether additional environmental and physical geographical variables, such as island isolation, elevation, climate and environmental heterogeneity, might explain the variation in species richness across small islands and whether their effect differs among growth forms.

2 | MATERIALS AND METHODS

2.1 | Data acquisition

For 953 islands belonging to 72 archipelagos worldwide, we extracted angiosperm species richness deconstructed into growth forms (herb, shrub and tree) and environmental island data from the Global Inventory

of Floras and Traits - GIFT database v.1.0 (Weigelt, König, & Krefl, 2020). The GIFT database collates species occurrences and functional traits from regional plant checklists and floras and features species composition data for > 1,800 islands worldwide (for details on data processing, see Weigelt et al., 2020; a list of the data sources is given in Appendix 1).

We extracted information on island area (in square kilometres), island perimeter (in kilometres), annual precipitation (in millimetres per year), mean annual temperature (in degrees Celsius; Climatologies at high resolution for the earth's land surface areas CHELSA; Karger et al., 2017) and two isolation metrics, namely the distance of the island to the nearest mainland (ISO_{dist} ; in kilometres) and the proportion of area of surrounding landmass (following Weigelt & Krefl, 2013). The latter metric is based on the land masses of neighbouring mainlands and islands and was calculated as one minus the proportion of land area within buffer distances of 100 km (ISO_{100}) and 1,000 km ($ISO_{1,000}$) around each focal island. The ISO_{dist} metric describes island isolation only with regard to the nearest mainland. The $ISO_{1,000}$ metric includes neighbouring islands in addition to larger landmasses and mainlands. The ISO_{100} metric describes island isolation from the nearest islands mostly within an archipelago.

To account for the complexity of island coastlines, we calculated a shape index as follows: $shape\ index = P/[2 \times (\pi \times A)^{0.5}]$, where P is the island perimeter and A is island area (Patton, 1975). We obtained elevation data at a resolution of 1 arc-s from the Shuttle Radar Topography Mission (<https://earthdata.nasa.gov>), extracted mean and maximum elevation, and calculated the terrain ruggedness index (Wilson, O'Connell, Brown, Guinan, & Grehan, 2007) for each island to account for the topographical heterogeneity of the islands, using the R package *raster* (Hijmans, 2019).

2.2 | Island selection

We used the following criteria to subset the data. First, as fine-scale elevation data were available only for landmasses between 60° N and 60° S, we excluded all islands located further north or south. Second, we included only islands for which we had growth form data for $\geq 75\%$ of all species. We used a threshold of 75% coverage because values of $\geq 70\%$ (Penone et al., 2014) to 80% (Májeková et al., 2016; Pakeman & Quested, 2007) are recommended for unbiased analyses, and higher thresholds would have led to omission of many more islands from the dataset. Third, we included only islands < 100 km², because species richness on larger islands is influenced by *in situ* speciation, affecting the shape of the SAR towards a third phase (Lomolino, 2000). This threshold is much larger than the SIE breakpoint area commonly reported for plants [mean .016 km², 95% confidence interval (CI): .001, .3 km²; Chisholm et al., 2016], but small enough to exclude islands with a high probability of *in situ* speciation (Kisel & Barraclough, 2010) and where *in situ* speciation is likely to influence the shape of the SAR (Lomolino, 2000; see the Supporting Information Supplementary Discussion on the selection of the island area threshold and Figures S1 and S2 for results obtained using a 1,000 km² threshold). Fourth, given that we analysed the shape of the SAR at the level of

single archipelagos, we included only archipelagos containing ≥ 10 islands. In total, 700 islands from 17 archipelagos met our criteria and were included in all subsequent analyses (for all islands and their attributes, see Table S1). This subset of islands also included empty islands, which are important for the correct detection of the SIE (Dengler, 2010; Wang et al., 2016).

2.3 | Species–area relationships and statistical analyses

To test for the presence of the SIE, we used an approach based on comparisons of alternative species–area models (e.g., Dengler, 2010; Matthews et al., 2014) using the Akaike information criterion (AIC; Burnham & Anderson, 2002). We calculated two breakpoint models and one linear model for total species richness and for the species richness of herbs, shrubs and trees, respectively (hereafter referred to as growth forms) as the response variable and \log_{10} -transformed island area as the explanatory variable for all archipelagos separately. The first breakpoint model had a zero slope before the breakpoint describing an SIE, where species richness varies independently of island area (Lomolino, 2000; Niering, 1963). The second breakpoint model allowed for two different slopes, where species richness increases with area at a different rate for smaller islands than for larger islands (Dengler, 2010; Gentile & Argano, 2005; Matthews et al., 2014). Breakpoint models were calculated using the R package *segmented* (Muggeo, 2008). The model with the lowest AIC was identified as the best-fitting model and used for all subsequent analyses. If a breakpoint model received more support than the linear model, we inferred the existence of an SIE. We used the position of the breakpoint (island area in square kilometres) to define the maximum island area up to which the SIE extends for the respective archipelago.

To test whether the breakpoint areas differ between growth forms, we applied paired *t*-tests on the breakpoint area values between all growth form combinations. To test whether the breakpoint area varies with isolation, we applied linear models of breakpoint areas (\log_{10} -transformed) as response and isolation metrics [ISO_{dist} (\log_{10} -transformed), ISO_{100} and $ISO_{1,000}$] as predictor variables. Isolation per archipelago was calculated as the mean isolation of all included islands.

We selected all islands that fell within the range of the SIE for each archipelago, to test which factors determine species richness on small islands. We applied linear mixed-effect models using the package *lme4* (Bates, Maechler, Bolker, & Walker, 2014). Mixed-effect models constitute an effective modelling tool when groups of data points vary idiosyncratically (Bunnefeld & Phillimore, 2012). We therefore included the archipelagos to which the islands belong as a random effect in all models. We calculated all models based on Gaussian and negative binomial error distributions. For the Gaussian models, we \log_{10} -transformed species richness after adding a value of one to attain normality. The negative binomial models were fitted to untransformed species richness values. Given that both approaches yielded similar results, we discuss only the Gaussian models in the

following. Results obtained from negative binomial models can be found in the Supporting Information (Figure S3). As fixed effects, we included seven explanatory variables. To avoid issues arising from multicollinearity (Figure S4), we included only variables that were not strongly correlated, using a coefficient of correlation threshold of $|r| = .7$ (Dormann et al., 2013). Non-collinear variables included island area (\log_{10} -transformed), the shape index, annual precipitation and mean annual temperature. When variables were collinear, we included only the variable that we expected to be the most important for plant species richness on islands. Of the three correlated isolation metrics, we selected the metric ISO_{100} , because for small islands the landmasses in close vicinity are particularly important sources of colonization (Diver, 2008). From the variables describing island topography, we used maximum elevation, because it has been shown to influence plant species richness on islands (Ackerman et al., 2007; Keppel, Gillespie, Ormerod, & Fricker, 2016), and the mean terrain ruggedness index to quantify topographical heterogeneity (Riley, DeGloria, & Elliot, 1999). We standardized all variables to a mean of zero and a standard deviation of one and calculated standardized parameter estimates and their CIs for all variables from the full model using the package *broom* (Robinson & Hayes, 2019). All analyses were implemented in the statistical software R (v.3.5.2; R Core Team, 2019).

3 | RESULTS

Plant species richness on the islands ranged from zero (observed on 28 islands) to 817 species (island of Aegina, Greece). On average, herb richness was higher than shrub and tree richness (Figures 1 and 2; Figure S5). Fifty-eight per cent of all species were classified as herbs, 11.9% as shrubs and 13.4% as trees. For 16.7% of the species, we could not obtain growth form data.

For total species richness, we detected an SIE for 70.6% of the archipelagos. When dissecting species richness per island into herb, shrub and tree richness, 70.6, 58.8 and 52.9% of all archipelagos, respectively, showed an SIE (Figure 2). Both breakpoint models that indicate the presence of the SIE were equally common for all species, herbs and shrubs. For trees, the SIE describing no relationship between species richness and island area (the model with a zero slope before the breakpoint) was most common (66%; Figure 2; Table S2; the SIE for one exemplary archipelago is shown in Figure 1; for AIC values and R^2 for all models, see Table S3).

For those archipelagos exhibiting an SIE, the breakpoint area was larger for shrub and tree than for total and herb species richness. Total (mean breakpoint area 3.7 km^2 , $SE \pm 3.2 \text{ km}^2$) and herb species richness (mean breakpoint area $.7 \text{ km}^2$, $SE \pm .2 \text{ km}^2$) showed the lowest breakpoint area. Shrub (mean breakpoint area 4.5 km^2 , $SE \pm 3.8 \text{ km}^2$) and tree species richness (mean breakpoint area 5.7 km^2 , $SE \pm 4.2 \text{ km}^2$) had larger breakpoint areas (Figure 2), with the breakpoint area of tree species richness being significantly larger than the breakpoint area of total species richness ($p < .05$).

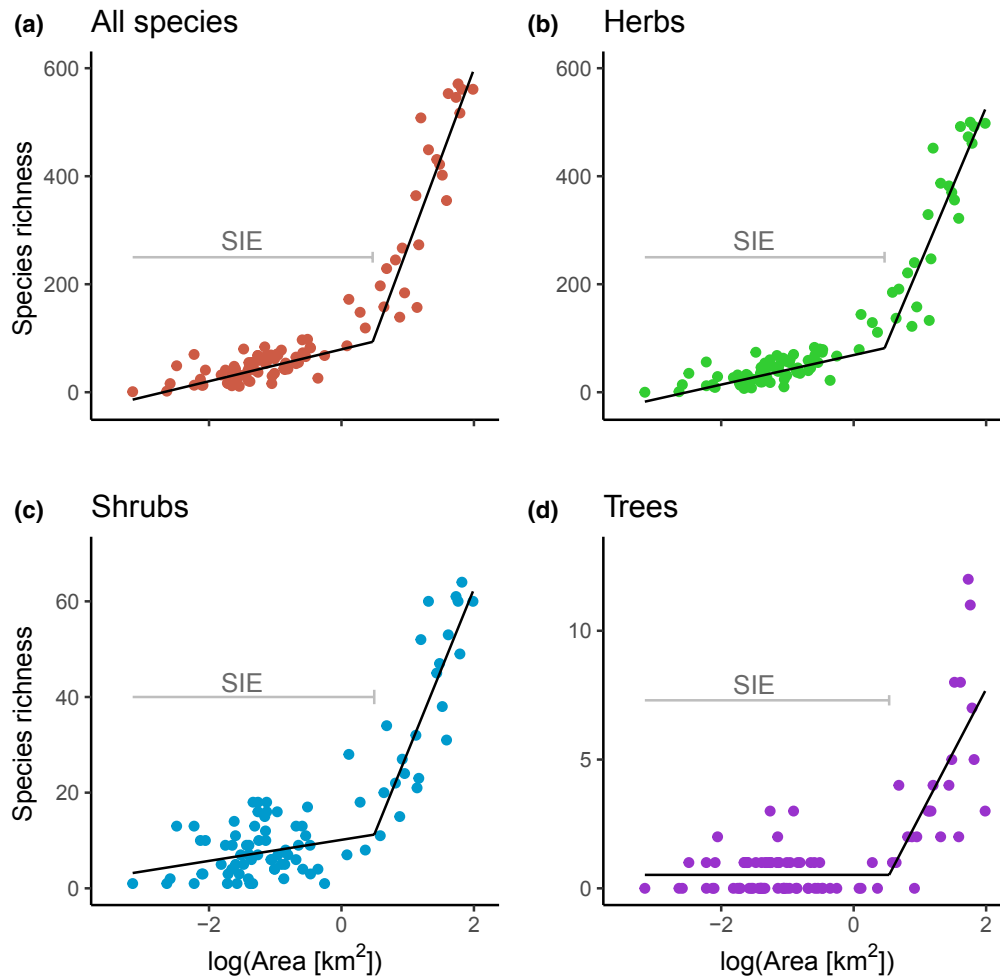


FIGURE 1 Best-supported species–area relationships (SARs), indicating the presence of a small-island effect (SIE) for (a) total species richness and for the species richness of (b) herbs, (c) shrubs and (d) trees from islands in the east Aegean Sea (island data from Kougioumoutzis et al., 2017). In this example, the best-fitting SAR model for total species richness and species richness of herbs and shrubs was a breakpoint model allowing for two distinct slopes, and a SAR model with a zero slope before the breakpoint for tree species richness [Colour figure can be viewed at wileyonlinelibrary.com]

We found contrasting effects of island isolation on the breakpoint areas for the different growth forms. In general, archipelagos with more isolated islands had larger breakpoint areas. Only ISO_{100} , which indicates the isolation of the islands within an archipelago, showed a significant effect on breakpoint area, which increased with isolation for total ($p < .05$; adjusted $R^2 = .33$) and for shrub species richness ($p < .05$; adjusted $R^2 = .36$). The breakpoint area for tree ($p = .28$; adjusted $R^2 = .05$) and herb species richness ($p = .53$; adjusted $R^2 = -.05$) was not significantly affected by ISO_{100} (Figure 3). The ISO_{dist} and $ISO_{1,000}$ did not explain the variation in the breakpoint areas between archipelagos (Figures S6 and S7).

Total species richness and species richness of the different growth forms on islands within the area range of the SIE were affected differentially by environmental factors. Total species richness was positively influenced by terrain ruggedness (estimate = .21; $SE \pm .09$). Herb species richness increased with island area (estimate = 1.62; $SE \pm .55$) and terrain ruggedness (estimate = .41; $SE \pm .17$) but decreased with mean annual temperature

(estimate = $-.82$; $SE \pm .40$). Shrub species richness increased with isolation (estimate = .32; $SE \pm .11$). Tree species richness responded strongly to annual precipitation (estimate = .41; $SE \pm .10$) and was highest on wet islands. The complexity of the shape of islands and their maximum elevation had little or no effect on species richness on small islands (Figure 4). The full models, with all fixed effects included for total species richness and species richness of the different growth forms, explained relatively small proportions of the variance. For total species richness, the marginal R^2 was 7.2%, for herb richness 15.9%, for shrub richness 16.9% and for tree richness 42.2%. The conditional R^2 values of the models were 66.6% for total species richness, 68.6% for herb richness, 45.8% for shrub richness and 81.0% for tree richness.

4 | DISCUSSION

The majority of archipelagos in our study featured an SIE, and the breakpoint area was affected by growth form and the isolation of

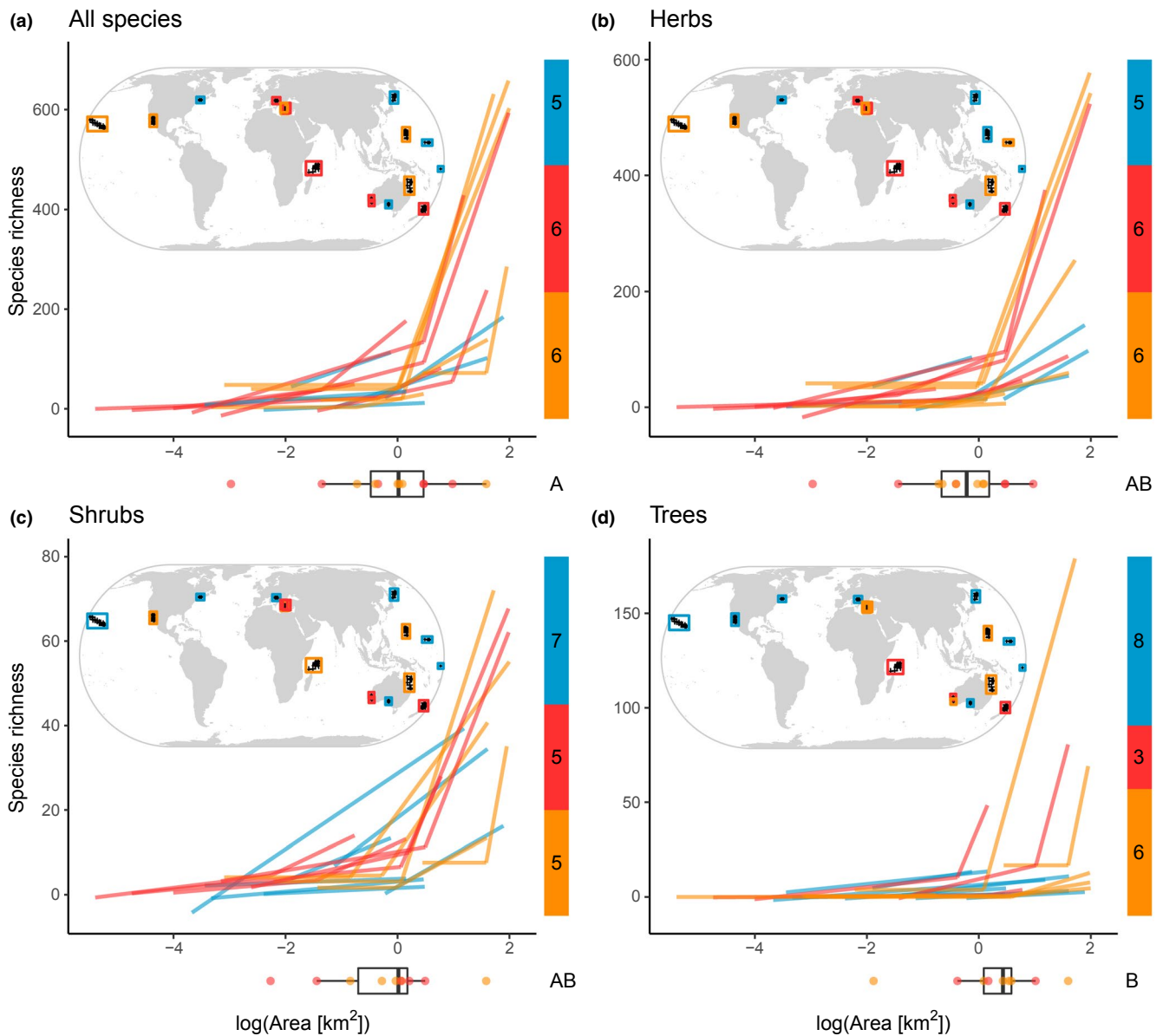


FIGURE 2 Species–area relationships (SARs) for (a) total species richness and for (b) herb, (c) shrub and (d) tree species richness for 17 archipelagos worldwide. Best-fitting SARs for each archipelago are shown. The SARs were fitted in semi-logarithmic space, and model selection was based on the Akaike information criterion. Candidate SARs consisted of one linear model (blue) and two breakpoint models that indicate the presence of the small-island effect (orange: zero slope before the breakpoint; red: breakpoint model allowing for two distinct slopes). Maps show the location of the archipelagos (rectangles). Colours of rectangles correspond to the colours of the best-fitting SARs. Note that two archipelagos in Western Australia and three archipelagos in the Aegean Sea partly overlap on the map. Model prevalence is indicated by numbers and coloured bars. Boxplots indicate the location of the breakpoint of the two breakpoint models, and capital letters indicate significant differences between groups calculated using Student's paired *t*-tests at the level of archipelagos (see also Table S4) [Colour figure can be viewed at wileyonlinelibrary.com]

the islands within an archipelago. We found evidence that the shape of the SAR, prevalence of the SIE and breakpoint area differed between total species richness and richness of herbs, shrubs and trees. Species richness on islands within the range of the SIE was differentially affected by environmental factors, possibly driven by different requirements of species with different growth forms. Overall, our results indicate that island biogeographical patterns differ between functional groups. We attribute these differences to different dispersal strategies and environmental requirements that become

evident at the level of growth forms but are disguised for total measures of species richness.

4.1 | Growth form influences the shape of the SAR

The prevalence of the SIE detected in our study was comparable to previous studies, which reported an SIE in 73–89% (Lomolino & Weiser, 2001) and 49% (Wang et al., 2016), respectively, for all

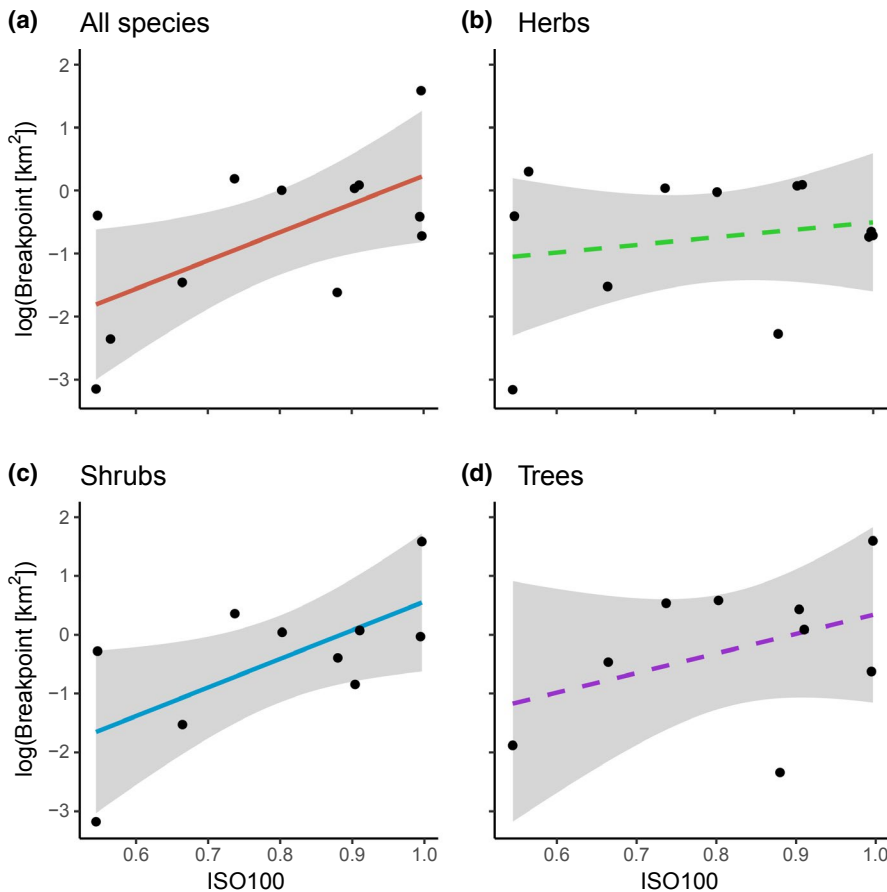


FIGURE 3 Relationship between archipelago isolation and breakpoint area of the small-island effect (SIE) for (a) total species richness and for the species richness of (b) herbs, (c) shrubs and (d) trees. Only archipelagos that featured an SIE were considered. The breakpoint area was determined by fitting breakpoint models. The ISO_{100} metric was calculated as one minus the mean landmass area within a buffer of 100 km per island, and refers to the proportion of ocean around all islands within an archipelago. Larger values indicate higher isolation of islands within an archipelago [Colour figure can be viewed at wileyonlinelibrary.com]

studied archipelagos. Our results therefore support the notion that the SIE is a widespread feature of archipelagos worldwide. Most archipelagos featured the SIE for total species richness and for the three growth forms. However, the SIE was less common for shrub and tree species richness than for total and herb species richness. Differences in the SIE prevalence between growth forms occurred mostly in a few archipelagos with low overall species richness, especially regarding shrub and tree species richness. It is possible that the low overall species richness of shrubs and trees in some archipelagos caused shallow SARs and prevented a biphasic SAR crucial to detect the SIE. The larger islands $< 100 \text{ km}^2$ of those archipelagos could therefore still be within the area range of the SIE for shrub and tree richness, causing a linear model to predict species richness best, although an SIE might prevail. However, also when including larger islands $\leq 1,000 \text{ km}^2$, the SIE was not more common for shrubs and trees (Supplementary Discussion and Figures S1 and S2). The similarity in form and shape of the SARs and the prevalence of the SIE for total and herb species richness can be explained by total species richness being dominated by herbs, which were the most species-rich growth form.

The location of the breakpoint area of the SIE differed considerably among plant growth forms and increased with the degree of isolation of the islands within an archipelago (hereafter: isolation), especially for total and shrub species richness (Figure 1). This finding is in line with the equilibrium theory of island biogeography

(MacArthur & Wilson, 1963). MacArthur and Wilson (1967) hypothesized that the SIE occurs when extinction events outnumber colonization events on small islands, decreasing the slope of the SAR towards low richness values. Thus, species groups with high dispersal abilities or low extinction probabilities should show smaller breakpoint areas, due to extinction rates being greater than colonization rates only on very small islands. In contrast, weak dispersers and species groups with high extinction probabilities should show larger breakpoint areas. It is possible that herbs are, on average, better dispersers than shrubs or trees (Tamme et al., 2014) and can maintain higher population densities within limited areas owing to their smaller size, thus decreasing their extinction probability on small islands (Pimm, Jones, & Diamond, 1988). Consequently, herbs may reach small islands more easily and may form less extinction-prone populations (see also Negoita et al., 2016), decreasing the breakpoint area of the SIE. Shrubs and trees may have lower immigration rates and require larger islands to establish persistent populations and, consequently, exhibit larger breakpoint areas. These patterns are enhanced by the degree of isolation (Negoita et al., 2016), with more isolated archipelagos having fewer immigration events, causing larger breakpoints (Ackerman et al., 2007; Lomolino & Weiser, 2001). However, whether island immigration rates and inter-island dispersal abilities differ between growth forms remains speculative and should be investigated more rigorously in the future.

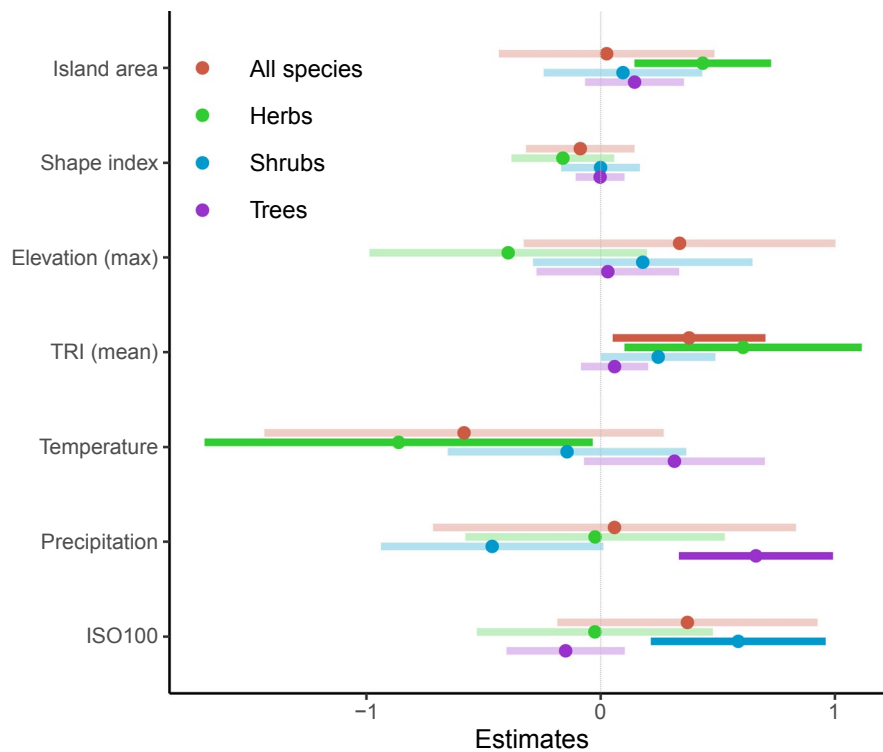


FIGURE 4 Standardized parameter estimates (dots) and confidence intervals (whiskers) for seven predictor variables of total species richness and for the richness of herbs, shrubs and trees on islands within the area range of the small-island effect. Positive estimates indicate that the respective variable led to an increase in species richness, negative estimates to a decrease. Linear mixed-effect models with all seven variables as predictors were used to calculate the estimates. Archipelago (not shown) was included as a random factor. Island area was \log_{10} -transformed. Shape index represents the edge-to-area ratio of the islands. TRI: is the mean terrain ruggedness index. Temperature and precipitation indicate the annual mean values for the islands. The ISO_{100} metric was calculated as the isolation, represented by one minus the buffer area ratio within 100 km around each island [Colour figure can be viewed at wileyonlinelibrary.com]

Interestingly, the SIE breakpoint area was significantly affected only by the isolation metric that considers small-scale variation in the proportion of neighbouring landmasses, that is, within 100 km buffer distances (ISO_{100}), whereas landmasses within larger buffer distances ($ISO_{1,000}$) and the distance to the nearest mainland (ISO_{dist}) had no effect on the breakpoint area (Figure 3). Small islands generally support less stable populations with high temporal species turnover (Chiarucci et al., 2017; Heatwole & Levins, 1973), which could be affected considerably by the degree of within archipelago isolation. Constant immigration from neighbouring islands or mainlands can counteract high extinction rates by promoting complex metapopulation systems (Burns & Neufeld, 2009; Hanski & Gilpin, 1991; Law et al., 2004) and source and sink dynamics (rescue effect; Brown & Kodric-Brown, 1977; Pulliam, 1988). Some of our analysed archipelagos were in close vicinity to large islands, such as the main islands of New Zealand, probably acting as a source pool for the small-island communities. This de-emphasizes the importance of the next mainland as the source pool for small islands which, in our example of New Zealand, would be Australia. Our results therefore highlight the scale-dependent influence of isolation and that consideration of small-scale spatial arrangements of neighbouring landmasses is important for explaining species richness on small islands (see also Weigelt & Kreft, 2013).

4.2 | Contrasting effects of environmental factors on species richness

The SIE posits that species richness on small islands is less dependent on area than it is on large islands (Dengler, 2010; Lomolino & Weiser, 2001; Triantis et al., 2006). However, which factors affect species richness on small islands or whether random processes dominate is still debated (Dengler, 2010; Menegotto, Rangel, Schrader, Weigelt, & Kreft, 2020; Schrader, König, et al., 2019; Triantis & Sfenthourakis, 2012; Triantis et al., 2006). Therefore, we tested for effects of different environmental, climatic and geographical variables on growth form species richness and found heterogeneous results (Figure 4). Among the environmental variables, topographical heterogeneity, a surrogate of habitat diversity, was the only important factor influencing the total species richness within the range of the SIE (see also Kohn & Walsh, 1994; Triantis et al., 2003). Species richness was affected by climatic variables for herb and tree richness and isolation for shrub richness. Indeed, the relatively strong influence of climatic variables on our results is supported by global trends in growth form composition (Hawkins, Rodríguez, & Weller, 2011; Keil & Chase, 2019; König et al., 2019). The positive relationship of shrub richness with isolation is possibly attributable to the fact that many of the most isolated islands in our dataset were atolls, which are

characterized by shrubby vegetation. Some shrubs are specialized for stressful environmental conditions on atolls (Stoddart, 1992), making them more competitive on isolated islands in comparison to herbs or trees.

The contrasting effects of environmental factors on small-island species richness highlight that herbs, shrubs and trees may have different environmental requirements (Echeverría-Londoño et al., 2018; Šimová et al., 2018). These requirements influence their group-specific species richness patterns and are not captured well by drivers of overall species richness. Possibly habitat diversity could serve as a good surrogate of the different aspect of species environmental requirements but might not be the ultimate driver of species richness on small islands for individual functional groups.

4.3 | Conclusion

Our results demonstrate that dissecting overall plant species richness into meaningful subgroups reveals complex biogeographical patterns. The shape of the SAR and the prevalence and breakpoint area of the SIE differ greatly among plant growth forms. This is driven by group-specific life-history characteristics and dispersal abilities and by environmental factors acting differentially on growth form species richness, highlighting ecological processes that are not discernible when using total measures of species richness. Overall, the SIE is a widespread phenomenon that is more complex than commonly anticipated. Our results highlight the potential of functional island biogeography for answering long-standing island biogeographical questions.

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AUTHOR CONTRIBUTIONS

J.S., H.K. and P.W. conceived the idea for this study; J.S., C.K., K.A.T., P.T. and P.W. collected the data; J.S. analysed the data and led the writing, with major contributions from all co-authors.

DATA AVAILABILITY STATEMENT

All data related to this article are included in the Supporting Information.

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REFERENCES

- Abbott, I., & Black, R. (1980). Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography*, 7, 399–410. <https://doi.org/10.2307/2844658>
- Ackerman, J. D., Trejo-Torres, J. C., & Crespo-Chuy, Y. (2007). Orchids of the West Indies: Predictability of diversity and endemism. *Journal of Biogeography*, 34, 779–786. <https://doi.org/10.1111/j.1365-2699.2006.01676.x>
- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. *Journal of Statistical Software*, 67, 1–23.
- Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, 58, 445–449. <https://doi.org/10.2307/1935620>
- Bunnefeld, N., & Phillimore, A. B. (2012). Island, archipelago and taxon effects: Mixed models as a means of dealing with the imperfect design of nature's experiments. *Ecography*, 35, 15–22. <https://doi.org/10.1111/j.1600-0587.2011.07078.x>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York: Springer.
- Burns, K. C., McHardy, R. P., & Pledger, S. (2009). The small-island effect: Fact or artefact? *Ecography*, 32, 269–276. <https://doi.org/10.1111/j.1600-0587.2008.05565.x>
- Burns, K. C., & Neufeld, C. J. (2009). Plant extinction dynamics in an insular metacommunity. *Oikos*, 118, 191–198. <https://doi.org/10.1111/j.1600-0706.2008.16816.x>
- Chiarucci, A., Fattorini, S., Foggi, B., Landi, S., Lazzaro, L., Podani, J., & Simberloff, D. (2017). Plant recording across two centuries reveals dramatic changes in species diversity of a Mediterranean archipelago. *Scientific Reports*, 7, 5415. <https://doi.org/10.1038/s41598-017-05114-5>
- Chisholm, R. A., Fung, T., Chimalakonda, D., & O'Dwyer, J. P. (2016). Maintenance of biodiversity on islands. *Proceedings of the Royal Society B: Biological Sciences*, 283, 1–8.
- Dengler, J. (2010). Robust methods for detecting a small island effect. *Diversity and Distributions*, 16, 256–266. <https://doi.org/10.1111/j.1472-4642.2010.00646.x>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- Diver, K. C. (2008). Not as the crow flies: Assessing effective isolation for island biogeographical analysis. *Journal of Biogeography*, 35, 1040–1048.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 027–046. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Duckworth, J. C., Kent, M., & Ramsay, P. M. (2000). Plant functional types: An alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography*, 24, 515–542. <https://doi.org/10.1191/030913300701542778>
- Echeverría-Londoño, S., Enquist, B. J., Neves, D. M., Violle, C., Boyle, B., Kraft, N. J. B., ... Kerkhoff, A. J. (2018). Plant functional diversity and the biogeography of biomes in North and South America. *Frontiers in Ecology and Evolution*, 6, 1–12. <https://doi.org/10.3389/fevo.2018.00219>
- Franzén, M., Schweiger, O., & Betzholtz, P. E. (2012). Species-area relationships are controlled by species traits. *PLoS ONE*, 7, 37359. <https://doi.org/10.1371/journal.pone.0037359>
- Gentile, G., & Argano, R. (2005). Island biogeography of the Mediterranean Sea: The species-area relationship for terrestrial isopods. *Journal of Biogeography*, 32, 1715–1726. <https://doi.org/10.1111/j.1365-2699.2005.01329.x>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary

- theory. *The American Naturalist*, 111, 1169–1194. <https://doi.org/10.1086/283244>
- Hanski, I., & Gilpin, M. E. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42, 3–16. <https://doi.org/10.1111/j.1095-8312.1991.tb00548.x>
- Hawkins, B. A., Rodríguez, M. Á., & Weller, S. G. (2011). Global angiosperm family richness revisited: Linking ecology and evolution to climate. *Journal of Biogeography*, 38, 1253–1266. <https://doi.org/10.1111/j.1365-2699.2011.02490.x>
- Heatwole, H., & Levins, R. (1973). Biogeography of the Puerto Rican Bank: Species-turnover on a small cay, Cayo Ahogado. *Ecology*, 54, 1042–1055. <https://doi.org/10.2307/1935570>
- Hijmans, R. J. (2019). raster: Geographic data analysis and modeling. R Package Version 3.0-7. Retrieved from <https://CRAN.R-project.org/package=raster>
- Höner, D., & Greuter, W. (1988). Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). *Vegetatio*, 77, 129–137. <https://doi.org/10.1007/BF00045758>
- Karger, D. N., Conrad, O., Böhrer, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler, M. (2017). Climatologies at high resolution for the Earth's land surface areas. *Scientific Data*, 4, 1–20. <https://doi.org/10.1038/sdata.2017.122>
- Keil, P., & Chase, J. M. (2019). Integrating global patterns and drivers of tree diversity across a continuum of spatial grains. *Nature Ecology and Evolution*, 3, 390–399.
- Keppel, G., Gillespie, T. W., Ormerod, P., & Fricker, G. A. (2016). Habitat diversity predicts orchid diversity in the tropical south-west Pacific. *Journal of Biogeography*, 43, 2332–2342. <https://doi.org/10.1111/jbi.12805>
- Kisel, Y., & Barraclough, T. G. (2010). Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, 175, 316–334. <https://doi.org/10.1086/650369>
- Knapp, A. K., Briggs, J. M., Collins, S. L., Archer, S. R., Bret-Harte, M. S., Ewers, B. E., ... Cleary, M. B. (2008). Shrub encroachment in North American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, 14, 615–623. <https://doi.org/10.1111/j.1365-2486.2007.01512.x>
- Kohn, D. D., & Walsh, D. M. (1994). Plant species richness – The effect of island size and habitat diversity. *Journal of Ecology*, 82, 367–377. <https://doi.org/10.2307/2261304>
- König, C., Weigelt, P., & Kreft, H. (2017). Dissecting global turnover in vascular plants. *Global Ecology and Biogeography*, 26, 228–242. <https://doi.org/10.1111/geb.12536>
- König, C., Weigelt, P., Schrader, J., Taylor, A., Kattge, J., & Kreft, H. (2019). Biodiversity data integration—The significance of data resolution and domain. *PLoS Biology*, 17, e3000183. <https://doi.org/10.1371/journal.pbio.3000183>
- Kougioumoutzis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660. <https://doi.org/10.1111/jbi.12920>
- Law, R., Tilman, D., Mouquet, N., Hoopes, M. F., Gonzalez, A., Amarasekare, P., ... Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lomolino, M. V. (1990). The target area hypothesis: The influence of island area on immigration rates of non-volant mammals. *Oikos*, 57, 297–300. <https://doi.org/10.2307/3565957>
- Lomolino, M. V. (2000). Ecology's most general, yet protean pattern: The species-area relationship. *Journal of Biogeography*, 27, 17–26.
- Lomolino, M. V., & Weiser, M. D. (2001). Towards a more general species-area relationship: Diversity on all islands, great and small. *Journal of Biogeography*, 28, 431–445. <https://doi.org/10.1046/j.1365-2699.2001.00550.x>
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387. <https://doi.org/10.1111/j.1558-5646.1963.tb03295.x>
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography* (1st ed.). Princeton, NJ: Princeton University Press.
- Májeková, M., Paal, T., Plowman, N. S., Bryndová, M., Kasari, L., Norberg, A., ... De Bello, F. (2016). Evaluating functional diversity: Missing trait data and the importance of species abundance structure and data transformation. *PLoS ONE*, 11, e0149270. <https://doi.org/10.1371/journal.pone.0149270>
- Matthews, T. J., Steinbauer, M. J., Tzirkalli, E., Triantis, K. A., & Whittaker, R. J. (2014). Thresholds and the species-area relationship: A synthetic analysis of habitat island datasets. *Journal of Biogeography*, 41, 1018–1028. <https://doi.org/10.1111/jbi.12286>
- Menegotto, A., Rangel, T. F., Schrader, J., Weigelt, P., & Kreft, H. (2020). A global test of the subsidized island biogeography hypothesis. *Global Ecology and Biogeography*, 29, 320–330.
- Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J., Dickie, J. B., & Westoby, M. (2005). A brief history of seed size. *Science*, 307, 576–580. <https://doi.org/10.1126/science.1104863>
- Morrison, L. W. (2011). Why do some small islands lack vegetation? Evidence from long-term introduction experiments. *Ecography*, 34, 384–391. <https://doi.org/10.1111/j.1600-0587.2010.06646.x>
- Muggeo, V. M. R. (2008). segmented: An R package to fit regression models with broken-line relationships. *R News*, 8, 20–25.
- Negoita, L., Fridley, J. D., Lomolino, M. V., Mittelhauser, G., Craine, J. M., & Weiher, E. (2016). Isolation-driven functional assembly of plant communities on islands. *Ecography*, 39, 1066–1077. <https://doi.org/10.1111/ecog.01551>
- Niering, W. A. (1963). Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs*, 33, 131–160. <https://doi.org/10.2307/1948559>
- Pakeman, R. J., & Quested, H. M. (2007). Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science*, 10, 91–96. <https://doi.org/10.1111/j.1654-109X.2007.tb00507.x>
- Panitsa, M., Tzanoudakis, D., & Sfenthourakis, S. (2008). Turnover of plants on small islets of the eastern Aegean Sea within two decades. *Journal of Biogeography*, 35, 1049–1061.
- Panitsa, M., Tzanoudakis, D., Triantis, K. A., & Sfenthourakis, S. (2006). Patterns of species richness on very small islands: The plants of the Aegean archipelago. *Journal of Biogeography*, 33, 1223–1234. <https://doi.org/10.1111/j.1365-2699.2006.01481.x>
- Patton, D. R. (1975). A diversity index for quantifying habitat “edge”. *Wildlife Society Bulletin*, 3, 171–173.
- Penone, C., Davidson, A. D., Shoemaker, K. T., Di Marco, M., Rondinini, C., Brooks, T. M., ... Costa, G. C. (2014). Imputation of missing data in life-history trait datasets: Which approach performs the best? *Methods in Ecology and Evolution*, 5, 961–970. <https://doi.org/10.1111/2041-210X.12232>
- Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Díaz, S., Kleyer, M., ... Tampucci, D. (2017). A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444–457. <https://doi.org/10.1111/1365-2435.12722>
- Pimm, S. L., Jones, H. L., & Diamond, J. M. (1988). On the risk of extinction. *The American Naturalist*, 132, 757–785. <https://doi.org/10.1086/284889>
- Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., ... Wright, I. J. (2008). Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology*, 89, 1908–1920. <https://doi.org/10.1890/07-0207.1>
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *The American Naturalist*, 132, 652–661. <https://doi.org/10.1086/284880>
- R Core Team. (2019). *R: A language and environment for statistical computing*. v.3.5.2. Vienna, Austria: R Foundation for Statistical Computing.

- Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *International Journal of Sciences*, *5*, 23–27.
- Robinson, D., & Hayes, A. (2019). *broom: Convert statistical analysis objects into tidy tibbles*. R package version 0.5.2. Retrieved from <https://CRAN.R-project.org/package=broom>
- Schrader, J., König, C., Moeljono, S., Pärtel, M., & Kreft, H. (2019). Requirements of plant species are linked to area and determine species pool and richness on small islands. *Journal of Vegetation Science*, *30*, 599–609. <https://doi.org/10.1111/jvs.12758>
- Schrader, J., Moeljono, S., Keppel, G., & Kreft, H. (2019). Plants on small islands revisited: The effects of spatial scale and habitat quality on the species–area relationship. *Ecography*, *42*, 1405–1414. <https://doi.org/10.1111/ecog.04512>
- Sfenthourakis, S., & Triantis, K. A. (2009). Habitat diversity, ecological requirements of species and the Small Island Effect. *Diversity and Distributions*, *15*, 131–140. <https://doi.org/10.1111/j.1472-4642.2008.00526.x>
- Si, X., Cadotte, M. W., Zeng, D., Baselga, A., Zhao, Y., Li, J., ... Ding, P. (2017). Functional and phylogenetic structure of island bird communities. *Journal of Animal Ecology*, *86*, 532–542. <https://doi.org/10.1111/1365-2656.12650>
- Šimová, I., Violle, C., Svenning, J. C., Kattge, J., Engemann, K., Sandel, B., ... Enquist, B. J. (2018). Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography*, *45*, 895–916. <https://doi.org/10.1111/jbi.13171>
- Stoddart, D. R. (1992). Biogeography of the Tropical Pacific! *Pacific Science*, *46*, 276–293.
- Tamme, R., Götzenberger, L., Zobel, M., Bullock, J. M., Hooftman, D. A. P., Kaasik, A., & Pärtel, M. (2014). Predicting species' maximum dispersal distances from simple plant traits. *Ecology*, *95*, 505–513. <https://doi.org/10.1890/13-1000.1>
- Thomson, F. J., Moles, A. T., Auld, T. D., Ramp, D., Ren, S., & Kingsford, R. T. (2010). Chasing the unknown: Predicting seed dispersal mechanisms from plant traits. *Journal of Ecology*, *98*, 1310–1318. <https://doi.org/10.1111/j.1365-2745.2010.01724.x>
- Tjørve, E., & Tjørve, K. M. C. (2011). Subjecting the theory of the small-island effect to Ockham's razor. *Journal of Biogeography*, *38*, 1834–1836. <https://doi.org/10.1111/j.1365-2699.2011.02534.x>
- Triantis, K. A., Mylonas, M., Lika, K., & Vardinoyannis, K. (2003). A model for the species–area–habitat relationship. *Journal of Biogeography*, *30*, 19–27. <https://doi.org/10.1046/j.1365-2699.2003.00805.x>
- Triantis, K. A., & Sfenthourakis, S. (2012). Island biogeography is not a single-variable discipline: The small island effect debate. *Diversity and Distributions*, *18*, 92–96. <https://doi.org/10.1111/j.1472-4642.2011.00812.x>
- Triantis, K. A., Vardinoyannis, K., Tsolaki, E. P., Botsaris, I., Lika, K., & Mylonas, M. (2006). Re-approaching the small island effect. *Journal of Biogeography*, *33*, 914–923. <https://doi.org/10.1111/j.1365-2699.2006.01464.x>
- Wang, Y., Millien, V., & Ding, P. (2016). On empty islands and the small-island effect. *Global Ecology and Biogeography*, *25*, 1333–1345. <https://doi.org/10.1111/geb.12494>
- Wang, Y., Wu, Q., Wang, X., Liu, C., Wu, L., Chen, C., ... Ding, P. (2015). Small-island effect in snake communities on islands of an inundated lake: The need to include zeroes. *Basic and Applied Ecology*, *16*, 19–27. <https://doi.org/10.1016/j.baae.2014.10.006>
- Weigelt, P., König, C., & Kreft, H. (2020). GIFT – A Global Inventory of Floras and Traits for macroecology and biogeography. *Journal of Biogeography*, *47*, 16–43.
- Weigelt, P., & Kreft, H. (2013). Quantifying island isolation – Insights from global patterns of insular plant species richness. *Ecography*, *36*, 417–429. <https://doi.org/10.1111/j.1600-0587.2012.07669.x>
- Westoby, M. (1998). A leaf-height–seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.
- Whitehead, D. R., & Jones, C. E. (1969). Small islands and the equilibrium theory of insular biogeography. *Evolution*, *23*, 171–179. <https://doi.org/10.1111/j.1558-5646.1969.tb03503.x>
- Whittaker, R. J. (1995). Disturbed island ecology. *Trends in Ecology and Evolution*, *10*, 421–425. [https://doi.org/10.1016/S0169-5347\(00\)89164-8](https://doi.org/10.1016/S0169-5347(00)89164-8)
- Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., ... Triantis, K. A. (2014). Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences USA*, *111*, 13709–13714. <https://doi.org/10.1073/pnas.1218036111>
- Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geodesy*, *30*, 3–35. <https://doi.org/10.1080/01490410701295962>
- Woodroffe, C. D. (1986). Vascular plant species–area relationships on Niu Atoll, Tuvalu, Central Pacific: A reassessment of the small island effect. *Australian Journal of Ecology*, *11*, 21–31.
- Wulfschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., ... Xu, X. (2014). Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, *114*, 1–16. <https://doi.org/10.1093/aob/mcu077>

BIOSKETCH

Julian Schrader is interested in biodiversity patterns and community assembly processes on islands. He uses plants as model organism to study changes in species richness and functional trait composition among islands. His research includes island ecology, functional biogeography and conservation biology, and he is especially interested in plant functional trait–environment dynamics.

SUPPORTING INFORMATION

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

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APPENDIX 1 DATA SOURCES

Island checklists

- Abbott, I., & Black, R. (1980). Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography*, *7*, 399–410.
- Amerson Jr., A. B. (1975). Species richness on the nondisturbed Northwestern Hawaiian Islands. *Ecology*, *56*, 435–444.
- Athens, J. S., Blinn, D. W., & Ward, J. V. (2007). Vegetation history of Laysan Island, Northwestern Hawaiian Islands. *Pacific Science*, *61*, 17–37.

- Batianoff, G. N., Naylor, G. C., Dillewaard, H. A., & Neldner, V. J. (2009). Plant strategies, dispersal and origins of flora at the northern Coral Sea Islands Territory, Australia. *Cunninghamia*, 11, 97–106.
- Batianoff, G. N., Neldner, V. J., Naylor, G. C., & Olds, J. A. (2012). *Mapping and evaluating Capricornia Cays vegetation and regional ecosystems*. Department of Science, Information Technology, Innovation and the Arts, Queensland Government, Brisbane, Australia.
- Brofas, G., Karetsos, G., Panitsa, M., & Theocharopoulos, M. (2001). The flora and vegetation of Gyalí Island, SE Aegean, Greece. *Willdenowia*, 31, 51–70.
- Burton, R. M. (1991). A check-list and evaluation of the flora of Nisyros (Dodecanese, Greece). *Willdenowia*, 20, 15–38.
- Cameron, E. K. (1984). Vascular plants of the three largest Chickens (Marotere) islands: Lady Alice, Whatupuke, Coppermine: North-East New Zealand. *TANE*, 30, 53–75.
- Cameron, E. K. (1985). Vascular flora and vegetation of Rimariki and associated islands, Mimiwhangata, north-east New Zealand. *TANE*, 31, 47–74.
- Cameron, E. K. (1990). Vascular plants of the main northern Mokohinau Islands, North-East New Zealand. *TANE*, 32, 113–130.
- Cameron, E. K., de Lange, P. J., McCallum, J., Taylor, G. A., & Bellingham, P. J. (2007). Vascular flora and some fauna for a chain of six Hauraki Gulf islands east and southeast of Waiheke Island. *Auckland Botanical Society Journal*, 62, 136–156.
- Case, T. J., Cody, M. L., & Ezcurra, E. (2002). *A new island biogeography of the Sea of Cortés*. New York: Oxford University Press.
- Court, D. J., & Hardacre, A. K., Lynch, P. A. (1973). The vegetation of the Aldermen Islands: a reappraisal. *TANE*, 19, 41–60.
- de Sloover, J. R., & Liégeois, S. (1997). Eagle Island flora and vegetation (Queensland, Australia). *Nationale Plantentuin van België*, 66, 347–383.
- Esler, A. E. (1978). Botanical features of the Mokohinau Islands. *TANE*, 24, 187–197.
- Fosberg, F. R. (1985). Vegetation of Bikini Atoll. *Atoll Research Bulletin*, 315, 1–28.
- Fosberg, F. R., Renvoize, S. A., & Townsend, C. C. (1980). *The flora of Aldabra and neighbouring islands*. London, UK: HMSO.
- Gage, S., Joneson, S. L., Barkalov, V. Y., Eremenko, N. A., & Takahashi, H. (2006). A newly compiled checklist of the vascular plants of the Habomais, the Little Kurils. *Bulletin of the Hokkaido University Museum*, 3, 67–91.
- Gerlach, J. (2003). The biodiversity of the granitic islands of Seychelles. *Phelsuma*, 11 (Supplement A), 1–47.
- Hill, M. J. (Ed.) (2002). *Biodiversity surveys and conservation potential of inner Seychelles islands*. Washington, DC: Smithsonian Institution.
- Imada, C. T. (Ed.) (2012). *Hawaiian native and naturalized vascular plants checklist*, (December 2012 update). Honolulu, Hawai'i: Hawaii Biological Survey, Bishop Museum.
- Jacks, B. R. (2010). *Plants of Magnetic Island* (3rd ed.). Townsville, Queensland, Australia: James Cook University.
- Jasprica, N., Dolina, K., & Milović, M. (2015). Plant taxa and communities on three islets in south Croatia, NE Mediterranean. *Natura Croatica*, 24, 191–213.
- Kamari, G., Phitos, D., Snogerup, B., & Snogerup, S. (1988). Flora and vegetation of Yioura, N Sporades, Greece. *Willdenowia*, 17, 59–85.
- Kougioumoutzis, K., Valli, A. T., Georgopoulou, E., Simaiakis, S. M., Triantis, K. A., & Trigas, P. (2017). Network biogeography of a complex island system: The Aegean Archipelago revisited. *Journal of Biogeography*, 44, 651–660. <https://doi.org/10.1111/jbi.12920>
- McCrea, J. (2003). *Inventory of the land conservation values of the Houtman Abrolhos Islands*. Perth, Western Australia, Australia: Department of Fisheries, Government of Western Australia.
- Negoita, L., Fridley, J. D., Lomolino, M. V., Mittelhauser, G., Craine, J. M., & Weiher, E. (2016). Isolation-driven functional assembly of plant communities on islands. *Ecography*, 39, 1066–1077.
- Ogle, C. C. (2002). *Checklist of vascular plants of Sugar Loaf Islands*. Wanganui Plant List, 61, 1–8. Department of Conservation. New Zealand.
- Pandža, M. (2002). Flora of the small islands of Murter. *Natura Croatica*, 11, 77–101.
- Pandža, M. (2003). Flora of the island of Zirje and the small islands around it (eastern Adriatic coast, Croatia). *Acta Botanica Croatia*, 62, 115–139.
- Pandža, M., & Milović, M. (2015a). Flora of the islets near Pakoštane (Dalmatia, Croatia). *Natura Croatica*, 24, 19–35.
- Pandža, M., & Milović, M. (2015b). Flora of the Veliki Lagan and Mali Lagan islets (Dugi Otok island, Croatia). *Natura Croatica*, 24, 215–222.
- Pandža, M., Milović, M., Kripina, & Tafra, D. (2011). Vascular flora of the Vrgada islets (Zadar Archipelago, Eastern Adriatic). *Natura Croatica*, 20, 97–116.
- Pandža, M., & Skvorc, Z. (2002). The flora of some uninhabited Sibenik Archipelago islands (Dalmatia, Croatia). *Natura Croatica*, 11, 367–385.
- Panitsa, M., Bazos, I., Dimopoulos, P., Zervou, S., Yannitsaros, A., & Tzanoudakis, D. (2004). Contribution to the study of the flora and vegetation of the Kithira Island group. Offshore Islets of Kithira (S Aegean, Greece). *Willdenowia*, 34, 101–115.
- Raulerson, L. (2006). Checklist of plants of the Mariana Islands. *University of Guam Herbarium Contribution*, 37, 1–69.
- Renvoize, S. A. (1975). A floristic analysis of the western Indian Ocean coral islands. *Kew Bulletin*, 30, 133–152.
- Robinson, A. C., Canty, P. D., & Fotheringham, D. (2008). Investigator group expedition 2006 flora and vegetation. *Transactions of the Royal Society of South Australia*, 132, 173–220.
- Robinson, A. C., Canty, P. D., Wace, N. M., & Barker, R. M. (2003). The encounter 2002 expedition to the isles of St Francis, South Australia. Flora and vegetation. *Transactions of the Royal Society of South Australia*, 127, 107–128.
- Skelin, M., Ljubičić, I., Skelin, I., Vitasović Kosić, I., & Bogdanović, S. (2014). The flora of Zečevo (Hvar Archipelago, Croatia). *Agriculturae Conspectus Scientificus*, 79, 85–91.
- Takahashi, H., Barkalov, V. Y., Gage, S., Joneson, S., Ilushko, M., & Zhuravlev, Y. N. (2002). A floristic study of the vascular plants of Raikoke, Kuril Islands. *Acta Phytotaxonomica et Geobotanica*, 53, 17–33.

- Takahashi, H., Barkalov, V. Y., Gage, S., Semsrott, B., Ilushko, M., & Zhuravlev, Y. N. (1999). A preliminary checklist of the vascular plants of Chirinkotan, Kuril Islands. *Journal of Phytogeography and Taxonomy*, 47, 131–137.
- Takahashi, H., Barkalov, V. Y., Gage, S., Semsrott, B., Ilushko, M., & Zhuravlev, Y. N. (2006). A floristic study of the vascular plants of Kharimkotan, Kuril Islands. *Bulletin of the Hokkaido University Museum*, 3, 41–66.
- Takahashi, H., Barkalov, V. Y., Gage, S., & Zhuravlev, Y. N. (1997). A preliminary study of the flora of Chirpoi, Kuril Islands. *Acta Phytotaxonomica et Geobotanica*, 48, 31–42.
- Tatewaki, M. (1957). Geobotanical studies on the Kurile Islands. *Acta Horti Gotoburgensis*, 21, 43–123.
- Taylor, G. A. (1991). Flora and fauna of Plate (Motunau) Island, Bay of Plenty. *TANE*, 33, 113–120.
- Taylor, G. A., & Lovegrove, T. G. (1997). Flora and vegetation of Stanley (Atiu) Island, Mercury Islands. *TANE*, 36, 85–111.
- Taylor, G. A., Lovegrove, T. G., Miskelly, C. M., McFadden, I., & Whitaker, A. H. (1987). An ecological survey of small islands in the Mercury Group. *TANE*, 32, 151–167.
- Velarde, E., Wilder, B. T., Felcer, R. S., & Ezcurra, E. (2014). Floristic diversity and dynamics of Isla Rasa, Gulf of California – A globally important seabird island. *Botanical Sciences*, 92, 89–101.
- Wagner, W. L., Herbst, D. R., & Lorence, D. H. (2005). Flora of the Hawaiian Islands website. Retrieved from <http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/>
- Walker, T. A. (1991). Pisonia Islands of the Great Barrier Reef. Part III. Changes in the vascular Flora of Lady Musgrave Island. *Atoll Research Bulletin*, 350, 31–41.
- Walker, T. A., Chaloupka, M. Y., & King, B. R. (1991). Pisonia Islands of the Great Barrier Reef. Part II. The vascular Floras of Bushy and Redbill Islands. *Atoll Research Bulletin*, 350, 24–30.
- Woodroffe, C. D. (1986). Vascular plant species-area relationships on Nui Atoll, Tuvalu, Central Pacific: a reassessment of the small island effect. *Australian Journal of Ecology*, 11, 21–31.
- Plant growth from data**
- 3D Environmental (2013). *Profile for management of the habitats and related ecological and cultural resource values of Boigu Island*. Torres Strait Regional Authority Land & Sea Management Unit. Australia.
- Abdel Khalik, K., El-Sheikh, M., & El-Aidarous, A. (2013). Floristic diversity and vegetation analysis of Wadi Al-Noman, Mecca, Saudi Arabia. *Turkish Journal of Botany*, 37, 894–907.
- Alves, R. J. V., & Kolbek, J. (2009). Summit vascular flora of Serra de São José, Minas Gerais, Brazil. *Check List*, 5, 35–73.
- Arakaki, M., & Cano, A. (2003). Composición florística de la cuenca del río Ilo-Moquegua y Lomas de Ilo, Moquegua, Peru. *Revista Peruana de Biología*, 10, 5–19.
- Assédé, E. P. S., Adomou, A. C., & Sinsin, B. (2012). Magnoliophyta, Biosphere Reserve of Pendjari, Atacora Province, Benin. *Check List*, 8, 642–661.
- Badshah, L., Hussain, F., & Sher, Z. (2013). Floristic inventory, ecological characteristics and biological spectrum of rangeland, District Tank, Pakistan. *Pakistan Journal of Botany*, 45, 1159–1168.
- Bancheva, S., & Vassilev, K. (2006). Vascular flora of the Beli Lom Nature Reserve in Northeast Bulgaria. *Phytologia Balcanica*, 12, 377–386.
- Benito, B. M., Lorite, J., Pérez-Pérez, R., Gómez-Aparicio, L., Peñas, J., & Robertson, M. (2014). Forecasting plant range collapse in a mediterranean hotspot. When dispersal uncertainties matter. *Diversity and Distributions*, 20, 72–83.
- Bernal, R., Gradstein, S. R., & Celis, M. (2015). Catálogo de plantas y líquenes de Colombia. Retrieved from <http://catalogoplantasdecolumbia.unal.edu.co/>
- BGCI (2017). GlobalTreeSearch online database. Retrieved from <https://www.bgci.org/resources/bgci-databases/>
- BioScripts (2014). Flora Vascular. Retrieved from <http://www.floravascular.com/>
- Botanical Garden Tel Aviv. (2019). Israel Flora: Tel Aviv University. Unpublished.
- Brennan, K. (1996). *An annotated checklist of the vascular plants of the Alligator Rivers Region, Northern Territory, Australia*. Barton, ACT, Australia.
- Bridgewater, S. G. M., Harris, D. J., Whitefoord, C., Monro, A. K., Penn, M. G., Sutton, D. A., ... Holst, B. K. (2006). A preliminary checklist of the vascular plants of the Chiquibul Forest, Belize. *Edinburgh Journal of Botany*, 63, 269–321.
- Brundu, G., & Camarda, I. (2013). The Flora of Chad: a checklist and brief analysis. *Phytokeys*, 23, 1–17.
- Bundesamt für Naturschutz. (2016). Floraweb. Retrieved from www.floraweb.de
- Cascante-Marín, A., & Estrada-Chavarría, A. (2012). Las plantas vasculares de El Rodeo, Costa Rica. *Brenesia*, 77, 71–128.
- Catarino, L., Martins, E. S., Basto, M. F., & Diniz, M. A. (2008). An annotated checklist of the vascular flora of Guinea-Bissau (West Africa). *Blumea-Biodiversity, Evolution and Biogeography of Plants*, 53, 1–222.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Amy, E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.
- Chawla, A., Parkash, O., Sharma, V., Rajkumar, S., Lal, B., Gopichand, Singh, R. D., & Thukral, A. K. (2012). Vascular plants, Kinnaur, Himachal Pradesh, India. *Check List*, 8, 321–348.
- Chinese Virtual Herbarium. (2016). *The Flora of China v.5.0*. Retrieved from http://www.efloras.org/flora_page.aspx?flora_xml:id=2
- Chong, K. Y., Tan, T. W. H., & Corlett, R. T. (2009). *A checklist of the total vascular plant flora of Singapore. Native, naturalised and cultivated species*. Singapore: Raffles Museum of Biodiversity Research.
- Clark, J. L., Neill, D. A., & Asanza, M. (2006). Floristic checklist of the Mache-Chindul mountains of Northwestern Ecuador. *Contributions from the United States National Herbarium*, 54, 1–180.
- Cochard, R., & Bloesch, U. (2007). Electronic plant species database of the Saadani National Park, coastal Tanzania. Retrieved from <http://www.wildlife-baldus.com/saadani.html>
- Costion, C., & Lorence, D. (2012). The endemic plants of Micronesia. A geographical checklist and commentary. *Micronesica*, 43, 51–100.

- Da Vela, M., Frignani, F., Bonari, G., & Angiolini, C. (2013). La flora vascolare della diserva naturale "La Pietra" (Toscana meridionale). *Micologia e Vegetazione Mediterranea*, 28, 135–160.
- Dauby, G., Leal, M., & Stevart, T. (2008). Vascular plant checklist of the coastal National Park of Pongara, Gabon. *Systematics and Geography of Plants*, 78, 155–216.
- Dauby, G., Zaiss, R., Blach-Overgaard, A., Catarino, L., Damen, T., Deblauwe, V., ... Couvreur, T. L. P. (2016). RAINBIO. A mega-database of tropical African vascular plants distributions. *PhytoKeys*, 74, 1–18.
- De Egea, J., Peña-Chocarro, M., Espada, C., & Knapp, S. (2012). Checklist of vascular plants of the Department of Ñeembucú, Paraguay. *Phytokeys*, 9, 15–179.
- de la Luz, L., Rebman, J., Domínguez-León, M., & Domínguez-Cadena, R. (2008). The vascular flora and floristic relationships of the sierra de la Giganta in Baja California Sur, México. *Revista Mexicana de Biodiversidad*, 79, 29–65.
- Desmet, P., & Brouillet, L. (2013). Database of Vascular Plants of Canada (VASCAN): a community contributed taxonomic checklist of all vascular plants of Canada, Saint Pierre and Miquelon, and Greenland. *Phytokeys*, 25, 55–67.
- Dimopoulos, P., Raus, T., Bergmeier, E., Constantinidis, T., Iatrou, G., Kokkini, S., ... Tzanoudakis, D. (2013). *Vascular plants of Greece. An annotated checklist*. Berlin, Germany: Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin; Athens, Greece: Hellenic Botanical Society.
- Domínguez, E., Marticorena, C., Elvebakk, A., & Pauchard, A. (2004). Catálogo de la flora vascular del Parque Nacional Pali Aike. XII Región, Chile. *Gayana Botánica*, 61, 67–72.
- Ejaz Ul Islam Dar, M., Cochard, R., Shrestha, R. P., & Ahmad, S. (2012). Floristic composition of Machiara National Park, District Muzaffarabad Azad Kashmir, Pakistan. *International Journal of Biosciences*, 2, 28–45.
- El-Ghani, M. M., & Abdel-Khalik, K. N. (2005). Floristic diversity and phytogeography of the Gebel Elba National Park, South-East Egypt. *Turkish Journal of Botany*, 30, 121–136.
- Engemann, K., Sandel, B., Boyle, B. L., Enquist, B. J., Jørgensen, P. M., Kattge, J., ... Svenning, J.-C. (2016). A plant growth form dataset for the New World. *Ecology*, 97, 3243.
- Espinosa-Jiménez, J. A., Pérez-Farrera, M. Á., & Martínez-Camilo, R. (2011). Inventario florístico del Parque Nacional Cañón del Sumidero, Chiapas, México. *Boletín de la Sociedad Botánica de México*, 89, 37–82.
- Fern, K., & Fern, A. (2015). Useful tropical plants database. Retrieved from: <http://tropical.theferns.info>
- Ferreira, A. L., Coutinho, B. R., Pinheiro, H. T., & Thomaz, L. D. (2007). Composição florística e formações vegetais da Ilha dos Franceses, Espírito Santo. *Boletim do Museu Biológico Mello Leitão*, 22, 25–44.
- Figueiredo, E., Paiva, J., Stevart, T., Oliveira, F., & Smith, G. F. (2011). Annotated catalogue of the flowering plants of São Tomé and Príncipe. *Bothalia*, 41, 41–82.
- Figueroa-C. Y., & Galeano, G. (2007). Lista comentada de las plantas vasculares del enclave seco interandino de La Tatacoa (Huila, Colombia). *Caldasia*, 29, 263–281.
- Fischer, E., Rembold, K., Althof, A., Obholzer, J., Malombe, I., Mwachala, G., ... Theisen, I. (2010). Annotated checklist of the vascular plants of Kakamega Forest, Western Province, Kenya. *Journal of East African Natural History*, 99, 129–226.
- Fischer, M. A., Adler, W., & Oswald, K. (2008). Exkursionsflora für Österreich, Liechtenstein und Südtirol. Bestimmungsbuch für alle in der Republik Österreich, im Fürstentum Liechtenstein und in der Autonomen Provinz Bozen, 3., verbesserte und erweiterte Auflage der "Exkursionsflora von Österreich". Landesmuseum, Linz.
- Gamit, S. B., Maurya, R. R., Qureshimatva, U. M., & Solanki, H. A. (2015). Check list of flowering plants in Tapi District, Gujarat, India. *International Journal of Advanced Research*, 3, 1104–1123.
- Gnoumou, A., Ouedraogo, O., Schmidt, M., & Thiombiano, A. (2015). Floristic diversity of classified forest and partial faunal reserve of Comoé-Léraba, southwest Burkina Faso. *Check List*, 11, 1557.
- Hauenstein, E., Muñoz-Pedreras, A., Yáñez, J., Sánchez, P., Möller, P., Guíñez, B., & Gil, C. (2009). Flora y vegetación de la Reserva Nacional Lago Peñuelas, Reserva de la Biósfera, Región de Valparaíso, Chile. *Bosque (Valdivia)*, 30, 159–179.
- Hawkins, B. A., Rueda, M., Rangel, T. F., Field, R., Diniz-Filho, J. A. F., & Linder, P. (2013). Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of North American forests. *Journal of Biogeography*, 41, 23–38.
- Heberling, J. M., Jo, I., Kozhevnikov, A., Lee, H., & Fridley, J. D. (2017). Biotic interchange in the Anthropocene: strong asymmetry in East Asian and eastern North American plant invasions. *Global Ecology and Biogeography*, 26, 447–458.
- Jardim Botânico do Rio de Janeiro (2016). *Flora do Brasil 2020 em construção*. Retrieved from <http://floradobrasil.jbrj.gov.br/>
- Jasprica, N., Dolina, K., & Milović, M. (2015). Plant taxa and communities on three islets in south Croatia, NE Mediterranean. *Natura Croatica*, 24, 191–213.
- Jiménez, J. E., Juárez, P., & Díaz, A. (2016). Checklist of the vascular flora of Reserva Biológica San Luis, Costa Rica. *Check List*, 12, 1859.
- Kabuye, C. H. S., Mungai, G. M., & Mutangah, J. G. (1986). Flora of Kora National Reserve. In M. Coe & N. M. Collins (Eds.), *Kora: an ecological inventory of the Kora National Reserve, Kenya. Kora research project 1982–85: a joint venture between the National Museums of Kenya and the Royal Geographical Society* (pp. 57–104). London: Royal Geographical Society.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., ... Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, 17, 2905–2935.
- Kim, C. S., Koh, J. G., Moon, M. O., Song, G. P., Hyun, H. J., Song, K. M., & Kim, M. H. (2007). Flora and life form spectrum of Hallasan natural reserve, Korea. *Journal of the Environmental Sciences*, 16, 1257–1269.
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., ... Peco, B. (2008). The LEDA Traitbase: a

- database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96, 1266–1274.
- Kraaij, T. (2011). The flora of the Bontebok National Park in regional perspective. *South African Journal of Botany*, 77, 455–473.
- Kumar, A., Bajpai, O., Mishra, A. K., Sahu, N., Behera, S. K., Bargali, S. S., & Chaudhary, L. B. (2015). A checklist of the flowering plants of Katerniaghat Wildlife Sanctuary, Uttar Pradesh, India. *Journal of Threatened Taxa*, 7, 7309–7408.
- Le Houerou, H.N. (2004). Plant diversity in Marmarica (Libya & Egypt): A catalogue of the vascular plants reported with their biology, distribution, frequency, usage, economic potential, habitat and main ecological features, with an extensive bibliography. *Candollea*, 59, 259–308.
- Limbu, D., Koirala, M., & Shang, Z. (2013). A checklist of Angiospermic Flora of Tinjure-Milke-Jaljale, Eastern Nepal. *Nepal Journal of Science and Technology*, 13, 87–96.
- Luke, Q. (2005). Annotated checklist of the plants of the Shimba Hills, Kwale District, Kenya. *Journal of East African Natural History*, 94, 5–120.
- Marticorena, C., Squeo, F. A., Arancio, G. & Muñoz, M. (2008). Catálogo de la flora vascular de la IV Región de Coquimbo. In F. A. Squeo, G. Arancio & J. R. Gutiérrez (Eds.), *Libro rojo de la flora nativa y de los sitios prioritarios para su conservación: Región de Atacama* (pp. 105–142). La Serena, Chile: Ediciones Universidad de La Serena.
- Marticorena, C., Stuessy, T. F., & Baeza, C. M. (1998). Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernández islands, Chile. *Gayana Botánica*, 55, 187–211.
- Masharabu, T. (2011). *Flore et végétation du Parc National de la Ruvubu au Burundi: diversité, structure et implications pour la conservation*. Dissertation. Université Libre de Bruxelles.
- Medjahdi, B., Ibn Tattou, M., Barkat, D., & Benabedli, K. (2009). La flore vasculaire des Monts des Trara (Nord Ouest Algérie). *Acta Botanica Malacitana*, 34, 57–75.
- Memariani, F., Joharchi, M. R., Ejtehadi, H., & Emadzadeh, K. (2009). Contributions to the flora and vegetation of Binalood Mountain range, NE Iran: Floristic and chorological studies in Fereizi region. *Ferdowsi University International Journal of Biological Sciences*, 1, 1–17.
- Norton, J., Majid, S. A., Allan, D., Al Safran, M., Böer, B., & Richer, R. A. (2009). *An illustrated checklist of the flora of Qatar*. Gosport, UK: Browndown Publications Gosport.
- Oliveira-Filho, A. T. (2014). *NeoTropTree. Flora arbórea da Região Neotropical: Um banco de dados envolvendo biogeografia, diversidade e conservação*. Retrieved from <http://www.icb.ufmg.br/treetan/>
- Pal, D., Kumar, A., & Dutt, B. (2014). Floristic diversity of Theog Forest Division, Himachal Pradesh, Western Himalaya. *Check List*, 10, 1083–1103.
- Pandža, M. (2002). Flora of the small islands of Murter. *Natura Croatica*, 11, 77–101.
- Pandža, M. (2003). Flora of the island of Zirje and the small islands around it (eastern Adriatic coast, Croatia). *Acta Botanica Croatia*, 62, 115–139.
- Pandža, M. (2010). Flora parka prirode Papuk (Slavonija, Hrvatska). *Šumarski List*, 134, 25–43.
- Pandža, M., & Milović, M. (2015a). Flora of the islets near Pakoštane (Dalmatia, Croatia). *Natura Croatica*, 24, 19–35.
- Pandža, M., & Milović, M. (2015b). Flora of the Veliki Lagan and Mali Lagan islets (Dugi Otok island, Croatia). *Natura Croatica*, 24, 215–222.
- Pandža, M., Milović, M., Kripina, & Tafra, D. (2011). Vascular flora of the Vrgada islets (Zadar Archipelago, Eastern Adriatic). *Natura Croatica*, 20, 97–116.
- Pandža, M., & Skvorc, Z. (2002). The flora of some uninhabited Sibenik Archipelago islands (Dalmatia, Croatia). *Natura Croatica*, 11, 367–385.
- Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, Ç., Lloret, F., Buhk, C., ... Rodrigo, A. (2009). Fire-related traits for plant species of the Mediterranean Basin. *Ecology*, 90, 1420.
- Pedashenko, H., & Vassilev, K. (2014). Flora of Ponor Special Protection Area (Natura 2000), western Bulgaria. *Acta Zoologica Bulgarica*, 5, 33–60.
- Peña-Chocarro, M. d. C. (2010). Updated checklist of vascular plants of the Mbaracayú Forest Nature Reserve (Reserva Natural del Bosque Mbaracayú), Paraguay. Auckland, New Zealand: Magnolia Press.
- Mahbubur Rahman, A. H. M. (2013). Angiospermic Flora of Rajshahi District, Bangladesh. *American Journal of Life Sciences*, 1, 105–112.
- Rahman, M. S., Hossain, G. M., Khan, S. A., & Uddin, S. N. (2015). An annotated checklist of the vascular plants of Sundarban mangrove forest of Bangladesh. *Bangladesh Journal of Plant Taxonomy*, 22, 17–41.
- Rossetto, E. F. S., & Vieira, A. O. S. (2013). Vascular flora of the Mata dos Godoy State Park, Londrina, Paraná, Brazil. *Check List*, 9, 1020–1034.
- Royal Botanic Gardens and Domain Trust. (2017). *PlantNET - The NSW Plant Information Network System*. Retrieved from <http://plantnet.rbgsyd.nsw.gov.au>
- SANBI. (2014). *Plants of Southern Africa. An online checklist*. Retrieved from <http://posa.sanbi.org>
- Schaefer, H., Hardy, O. J., Silva, L., Barraclough, T. G., & Savolainen, V. (2011). Testing Darwin's naturalization hypothesis in the Azores. *Ecology Letters*, 14, 389–396.
- Schönfelder, P., & Schönfelder, I. (1997). *Die Kosmos-Kanarenflora. Über 850 Arten der Kanarenflora und 48 tropische Ziergehölze*. Stuttgart, Germany: Franckh-Kosmos.
- Scoupe, M. (2011). *Composition floristique et diversité de la végétation de la zone Est du Parc National de Taï (Côte d'Ivoire)*. Doctoral dissertation, University of Geneva.
- Selvi, F. (2010). A critical checklist of the vascular flora of Tuscan Maremma (Grosseto province, Italy). *Flora Mediterranea*, 20, 47–139.
- Senterre, B., Chew, M. Y., & Chung, R. C. K. (2015). Flora and vegetation of Pulau Babi Tengah, Johor, Peninsular Malaysia. *Check List*, 11, 1714.
- Singh, A. (2015). Observations on the vascular flora of Banaras Hindu University Main Campus, India. *International Journal of Modern Biology and Medicine*, 6, 48–87.

- Skelin, M., Ljubičić, I., Skelin, I., Vitasović Kosić, I., & Bogdanović, S. (2014). The flora of Zečevo (Hvar Archipelago, Croatia). *Agriculturae Conspectus Scientificus*, 79, 85–91.
- Slik, F. J. W., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P., Alves, L. F., Ashton, P., ... Venticinque, E. M. (2015). An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 7472–7477.
- Smith, A. C. (1979–1996). *Flora Vitiensis nova. A new Flora of Fiji (spermatophytes only)*. Lawaii, Hawaii: Pacific Tropical Botanical Garden.
- Stalmans, M. (2006). *Tinley's plant species list for the Greater Gorongosa ecosystem, Moçambique*. Unpublished report by International Conservation Services to the Carr Foundation and the Ministry of Tourism.
- Tamis, W. L. M., van der Meijden, R., Runhaar, J., Bekker, R. M., Ozinga, W. A., Odé, B., & Hoste, I. (2004). Standard list of the flora of the Netherlands 2003. *Gorteria*, 30, 101–195.
- ter Steege, H., Vaessen, R. W., Cardenas-Lopez, D., Sabatier, D., Antonelli, A., de Oliveira, S. M., ... Salomao, R. P. (2016). The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Scientific Reports*, 6, 29549.
- Thiombiano, A., Schmidt, M., Dressler, S., Ouédraogo, A., & Hahn, K. (2012). Catalogue des plantes vasculaires du Burkina Faso. *Boissiera: mémoires des Conservatoire et Jardin botaniques de la Ville de Genève*, 65, 1–391.
- Tonkov, S., Pavlova, D., Atanassova, J., Nedelcheva, A., & Marinova, E. (2004). *Floristic catalogue of the nature reserve Rilomanastirska Gora (Central Rila Mountains). I. The locality Kirilova*. Sofia, Bulgaria: University of Sofia.
- Tropicos (2015). *Catálogo de las Plantas Vasculares de Bolivia*. St Louis, MO: Tropicos. Missouri Botanical Garden.
- Turner, I. M. (1995). *A catalogue of the vascular plants of Malaya*. Singapore: Gardens' Bulletin.
- Tutul, E., Uddin, M. Z., Rahman, M. O., & Hassan, M. A. (2009). Angiospermic flora of Runctia sal forest, Bangladesh. I. Liliopsida (Monocots). *Bangladesh Journal of Plant Taxonomy*, 16, 83–90.
- UIB (2007). *Herbario virtual del Mediterráneo Occidental*. Retrieved from <http://herbarivirtual.uib.es/ca>
- University of Greifswald (2010). *FloraGREIF - Virtual Flora of Mongolia*. Retrieved from <http://greif.uni-greifswald.de/floragreif/>
- USDA & NRCS (2015). *The PLANTS database*. Retrieved from <http://plants.usda.gov>
- Van Sam, Hoang. Uses and conservation of plant diversity in Ben En National Park, Viet Nam. National herbarium of the Netherlands, the Netherlands (2009).
- van Vreeswyk, A. M. E., Payne, A. L., Leighton, K. A., & Hennig, P. (2004). An inventory and condition survey of the Pilbara region, Western Australia, Perth. Technical Bulletin 92. Department of Agriculture.
- Vanderplank, S. E. (2010). *The vascular flora of Greater San Quintín, Baja California, Mexico*. Master Thesis. Claremont Graduate University.
- Velarde, E., Wilder, B. T., Felcer, R. S., & Ezcurra, E. (2014). Floristic diversity and dynamics of Isla Rasa, Gulf of California – A globally important seabird island. *Botanical Sciences*, 92, 89–101.
- Velarde, E. P., Guzmán, R. C., & Koch, S. D. (2008). Plantas vasculares y vegetación de la parte alta del Arroyo Agua Fria, municipio de Minatitlán, Colima, México. *Acta Botanica Mexicana*, 84, 25–72.
- VicFlora (2016). *Flora of Victoria*. Retrieved from <http://vicflora.rbg.vic.gov.au>
- Viciani, D., Gonnelli, V., Sirotti, M., & Agostini, N. (2010). An annotated check-list of the vascular flora of the “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (Northern Apennines Central Italy). *Webbia*, 65, 3–131.
- Vogt, C. (2011). Composición de la Flora Vascular del Chaco Boreal, Paraguay. I. Pteridophyta y Monocotiledoneae. *Steviana*, 3, 13–47.
- Wagner, W. L., Herbst, D. R., & Lorence, D. H. (2005). *Flora of the Hawaiian Islands website*. Retrieved from <http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/>
- WCSP (2014). *World checklist of selected plant families*. Retrieved from <http://apps.kew.org/wcsp/home.do>
- Western Australian Herbarium (2017). *FloraBase - The Western Australian flora*. Retrieved from <https://florabase.dpaw.wa.gov.au/>
- Woodroffe, C. D. (1986). Vascular plant species-area relationships on Nui Atoll, Tuvalu, Central Pacific: a reassessment of the small island effect. *Australian Journal of Ecology*, 11, 21–31.
- Yineger, H., Kelbessa, E., Bekele, T., & Lulekal, E. (2008). Floristic composition and structure of the dry afro-montane forest at Bale Mountains National Park, Ethiopia. *SINET: Ethiopian Journal of Science*, 31, 103–120.
- Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., ... Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92.
- Zhang, S.-B., Slik, J. W. F., Zhang, J.-L., & Cao, K.-F. (2011). Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Global Ecology and Biogeography*, 20, 241–250.
- Zhang, S. T., Zhen Du, G., & Chen, J. K. (2004). Seed size in relation to phylogeny, growth form and longevity in a subalpine meadow on the east of the Tibetan plateau. *Folia Geobotanica*, 39, 129–142.
- Zuloaga, F. O., Morrone, O., & Belgrano, M. (2014). *Catálogo de las Plantas Vasculares del Cono Sur*. Retrieved from <http://www.darwin.edu.ar/Proyectos/FloraArgentina/fa.htm>
- Zvyagintseva, K. O. (2015). An annotated checklist of the urban flora of Kharkiv. Kharkiv, Ukraine: Kharkiv National University.
- Артемюв, И. А. (2012). Определитель растений Катунского биосферного заповедника. БАРНАУЛ: Russian Academy of Sciences.