Remoteness promotes alien species richness on islands

Authors: Dietmar Moser[1,†], Bernd Lenzner[1,*,†], Patrick Weigelt[2], Wayne Dawson[3], Holger Kreft[2], Jan Pergl[4], Petr Pyšek[4,5,6], Mark van Kleunen[7,8], Marten Winter[9], César Capinha[10,11], Phillip Cassey[12], Stefan Dullinger[1], Evan P. Economo[13], Pablo García-Diaz[12, 14], Benoit Guénard[13,15], Florian Hofhansl[1], Thomas Mang[1], Hanno Seebens[16], Franz Essl[1]

Affiliations:

[1]Division of Conservation Biology, Vegetation and Landscape Ecology, University of Vienna, Rennweg 13, 1030 Vienna, Austria.

[2]Biodiversity, Macroecology and Biogeography, University of Goettingen, Büsgenweg 1, 37077 Göttingen, Germany.

[3]Department of Biosciences, Durham University, South Road, Durham, DH1 3LE, United Kingdom.

[4]Institute of Botany, Department of Invasion Ecology, The Czech Academy of Sciences, CZ-252 43 Průhonice, Czech Republic.

[5]Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic.

[6]Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Matieland 7602, South Africa.

[7]Ecology, University of Konstanz, Universitätsstrasse 10, 78457 Konstanz, Germany.

[8]Zhejiang Provincial Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou 318000, China.

[9]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, 04103 Leipzig, Germany.

[10]CIBIO/InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Cátedra REFER-Biodiversidade, Universidade do Porto, Campus Agrário de Vairão, 4485-661 Vairão, Portugal.

[11]Zoologisches Forschungsmuseum Alexander Koenig, Museumsmeile Bonn, 53113 Bonn, Germany.

[12]School of Biological Sciences and Centre for Conservation Science and Technology (CCoST), The University of Adelaide, North Terrace SA 5005, Australia

[13]Okinawa Institute of Science and Technology. Graduate University, 1919-1 Tancha, Onna, Okinawa, 904-0495, Japan.

[14] Landcare Research New Zealand, PO Box 69040, Lincoln 7640, New Zealand

[15]School of Biological Sciences, The University of Hong Kong, Hong Kong SAR, China.

[16]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany.

*Correspondence to: bernd.lenzner@univie.ac.at

†These authors contributed equally to the manuscript.

Abstract:

One of the most well-known and general patterns in island biogeography is the decrease in native species richness with isolation, reflecting lower rates of natural dispersal and colonization on remote oceanic islands [1,2]. During recent centuries, however, a novel, much faster process has increasingly gained importance and altered the composition and richness of island species pools: the human-mediated introduction of alien species[3–7]. Analyzing a comprehensive global dataset for alien and native plants, ants, reptiles and mammals on (sub-)tropical islands, we found that the number of alien species increases with isolation - a pattern that is opposite to the negative species-isolation relationship (SIR) of native species, and robust across all taxa analyzed. We argue that the reversal of the SIR for alien species is driven by a decrease in the resistance of resident biota to colonization by new species with increasing geographical isolation [8–10].

Main Text:

While the negative SIR for native species is one of the best documented patterns in ecology, it is less clear whether or how the number of alien species on islands is related to isolation. On the one hand, economic theory predicts that fewer commodities are transported to more remote islands[11], leading to fewer intentional and accidental alien introductions (i.e. lower propagule pressure), and hence arguably lower colonization rates [12]. On the other hand, globalization in trade and transport has considerably reduced the effective isolation worldwide – even of the most remote islands. While natural dispersal to remote islands is extremely rare and has led to the isolation effect in native species, human-aided transport increases the frequency of introduction events by orders of magnitude and the isolation effect might vanish[1]. Another line of reasoning suggests that establishment odds of the introduced alien species may be higher on more isolated islands if their impoverished and biologically naïve native biotas provide enhanced ecological opportunities for the introduced species [8–10]. Taken together, these theories would predict alien species richness on islands to be negatively, positively or uncorrelated with isolation, depending on the trade-offs between colonization pressure and establishment odds. Empirical studies have provided ambiguous results, with negative (for plants and birds [13]), no (for plants [14]) or positive (for birds [15], plants [16] and ants [17]) correlations between alien species and island isolation.

Here, we use the most comprehensive datasets currently available of established alien (*sensu* Blackburn et al.[18]) and native species numbers on islands to compare the importance of island isolation (i.e., distance to the closest mainland) for native and established alien species richness of vascular plants, ants, reptiles and mammals on subtropical and tropical islands (between 30°N and 30°S latitude; Fig. 1). In our analysis, we account for the effects of other important factors such as island size, climatic and topographic heterogeneity and human impact by using them as additional predictor variables in generalized linear mixed effects models.

Across all four taxonomic groups, we found that island isolation has contrasting effects on native and alien species richness. While native species richness decreased with isolation, confirming island-biogeography theory [1,2,19], alien species richness increased with isolation for all four taxonomic groups (only marginally significant for reptiles, Fig. 2 & 3, Table S1, S6). Consequently, when native and alien richness are considered together, we find a marked weakening of the SIRs compared to the pattern for natives only (Fig. 2 & 3, Table S1).

The effects of the other predictor variables on species richness were as expected: the numbers of both native and alien species increased with island area (Fig. 3, Table S1). Socioeconomic development (measured as per capita GDP) has a significant positive effect on alien species richness of all taxonomic groups, but it did not affect native species richness (Fig. 3, Table S1). For plants and mammals, per capita GDP was still significant when considering alien and native richness together. Due to the focus on (sub-)tropical islands, climate effects were minor; only native reptile species richness increased with mean annual temperature, and native ant and vascular plant species richness increased with annual precipitation (Fig. 3, Table S1). Finally, alien and native vascular plant and native mammal species richness were positively related to topographic heterogeneity (Fig. 3, Table S1). The robustness of our results was confirmed by a sensitivity analysis that removes potential biases introduced by differences in geographic coverage, sampling intensity and data quality (see Table S2).

One possible process behind the positive SIRs for alien species richness is a systematic decrease in the resistance of resident biota to the colonization by new species with increasing geographical isolation. This hypothesis was already formulated by Elton [8] and later explicated e.g., by Simberloff [9] and Denslow[10]. Arguments in favour of this idea emphasize that different resource-use of native and alien species is crucial for successful establishment of the latter [20], and that this divergence likely increases with geographical (and hence commonly evolutionary) isolation. Moreover, particular functional groups, especially large predators and herbivores [21], but also pathogens and parasites (e.g., [22]), are generally rarer or absent from remote islands. This leads to reduced predator-escape responses (e.g. island tameness in lizards [23]) and lower resistance to novel parasites in many native island species. As a consequence, introduced predators might have easier access to resident prey, and introduced prey might experience less predation pressure ("enemy release" hypothesis [24]). In addition, alien species introduce traits that native island biotas have not been exposed to previously (e.g., allelopathic secondary chemical compounds[25]) and to which they are naïve ("novel weapons" hypothesis [26]), a phenomenon that may increase with isolation as native species become more evolutionarily distinct [23]. Furthermore, as isolated islands usually have a reduced phylogenetic diversity[27], the species there might have experienced less competition, and therefore be competitively inferior to alien species from regions with a high phylogenetic diversity ("evolutionary imbalance" hypothesis[28]). Taken together, these mechanisms may well drive a strong positive correlation between geographical isolation and successful establishment of new arrivals, and hence drive the consistent positive alien species-isolation pattern found in our data.

Yet, variation in propagule and colonization pressure might also affect the establishment odds of alien species [12]. In a study on birds [15], the authors argue that remote islands generally lack native species useful for farming, hunting or aesthetic purposes, which might have led to a greater number of intentional releases of alien birds (i.e., higher colonization pressure), driving a positive SIR. The direct effect of colonization pressure, however, remains difficult to test, as for most taxonomic groups reliable data on introduction events do not exist. Introduction effort is positively correlated with GDP[29], and our analyses thus partly corrected for introduction effort by including GDP. Moreover, it seems unlikely that introduction effort (i.e. intentional releases) generally increases with geographic isolation for all tested taxonomic groups (especially for those introduced unintentionally like ants), and thus might have driven the positive SIRs.

In conclusion, alien species have markedly changed fundamental biogeographical patterns of island-species richness. The breakdown of biogeographic dispersal barriers, due to human transport, has weakened the classical SIRs. Indeed, the addition of alien species more than halves the effect of isolation on total species numbers. While this pattern has previously been shown for *Anolis* lizards in the Carribean[30], we here show that it holds globally for multiple taxonomic groups.

Globalization in trade and transport increasingly decouples geographical distance from isolation. As a consequence, immigration rates increase and geographically distant, but no longer isolated islands become packed with species as much as the theory of island biogeography would predict for equal-sized but less isolated islands[1] and may reach a new equilibrium, likely at the expense of many endemic species. However, even if globalization would completely neutralize geographic isolation and natural dispersal barriers, this might explain a weakening of the SIR slopes but not an inversion. Yet, there is a clear congruency of low native diversity and disproportionately high alien species numbers on remote islands. We thus argue that the inverted alien SIR is at least partially driven by a systematic increase in the invasibility due to a decrease in the resistance of resident biota with increasing geographical isolation.

References and Notes:

1. MacArthur, R. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton University Press, New Jersey, 1967).
2. Weigelt, P. & Kreft, H. Quantifying island isolation - insights from global patterns of insular plant species richness. *Ecography (Cop.).* **36,** 417–429 (2013).
3. Sax, D. F. & Gaines, S. D. Species invasions and extinction: the future of native biodiversity on islands. *Proc. Natl. Acad. Sci. U. S. A.* **105,** 11490–11497 (2008).
4. Capinha, C., Essl, F., Seebens, H., Moser, D. & Pereira, H. M. The dispersal of alien species redefines biogeography in the Anthropocene. *Science (80-.).* **348,** 1248–1251 (2015).
5. van Kleunen, M. *et al.* Global exchange and accumulation of non-native plants. *Nature* **525,** 100–103 (2015).
6. Dawson, W. *et al.* Global hotspots and correlates of alien species richness across taxonomic groups. *Nat. Ecol. Evol.* **1,** 186 (2017).
7. Seebens, H. *et al.* No saturation in the accumulation of alien species worldwide. *Nat. Commun.* **8,** 14435 (2017).
8. Elton, C. S. *The Ecology of Invasions by Animals and Plants*. (The University of Chicago Press, 1958). doi:10.1007/978-1-4899-7214-9
9. Simberloff, D. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Sci.* **49,** 87–97 (1995).
10. Denslow, J. S. Weeds in Paradise: Thoughts on the Invasibility of Tropical Islands. *Ann. Missouri Bot. Gard.* **90,** 119–127 (2003).
11. Deidda, M. Insularity and economic development: a survey. *Int. Rev. Econ.* **63,** 1–22 (2015).
12. Lockwood, J. L., Cassey, P. & Blackburn, T. M. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers. Distrib.* **15,** 904–910 (2009).
13. Blackburn, T. M., Delean, S., Pyšek, P., Cassey, P. & Field, R. On the island biogeography of aliens: a global analysis of the richness of plant and bird species on oceanic islands. *Glob. Ecol. Biogeogr.* **25,** 859–868 (2016).
14. Traveset, A., Kueffer, C. & Daehler, C. C. Global and regional nested patterns of non-native invasive floras on tropical islands. *J. Biogeogr.* **41,** 823–832 (2014).
15. Blackburn, T. M., Cassey, P. & Lockwood, J. L. The island biogeography of exotic bird species. *Glob. Ecol. Biogeogr.* **17,** 246–251 (2008).

16. Denslow, J. S., Space, J. C. & Thomas, P. a. Invasive exotic plants in the tropical pacific islands: Patterns of diversity. *Biotropica* **41,** 162–170 (2009).

17. Roura-Pascual, N., Sanders, N. J. & Hui, C. The distribution and diversity of insular ants: do exotic species play by different rules? *Glob. Ecol. Biogeogr.* **25,** 642–654 (2016).

18. Blackburn, T. M. *et al.* A proposed unified framework for biological invasions. *Trends Ecol. Evol.* **26,** 333–9 (2011).

19. Whittaker, R. J., Triantis, K. a. & Ladle, R. J. A general dynamic theory of oceanic island biogeography. *J. Biogeogr.* **35,** 977–994 (2008).

20. Drenovsky, R. E. *et al.* A functional trait perspective on plant invasion. *Ann. Bot.* **110,** 141–153 (2012).

21. Atkinson, I. A. E. in *Conservation for the twenty-first century* 54–69 (Oxford University Press, New York, 1989).

22. Apanius, V., Yorinks, N., Bermingham, E. & Ricklefs, R. E. Island and taxon effects in parasitism and resistance of Lesser Antillean birds. *Ecology* **81,** 1959–1969 (2000).

23. Cooper, W. E., Pyron, R. A. & Garland, T. Island tameness: living on islands reduces flight initiation distance. *Proc. Biol. Sci.* **281,** 20133019 (2014).

24. Keane, R. M. & Crawley, M. J. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17,** 164–170 (2002).

25. Cappuccino, N. & Arnason, J. T. Novel chemistry of invasive exotic plants. *Biol. Lett.* **2,** 189–193 (2006).

26. Callaway, R. M. & Ridenour, W. M. Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.* **2,** 436–443 (2004).

27. Weigelt, P. *et al.* Global patterns and drivers of phylogenetic structure in island floras. *Sci. Rep.* **5,** 12213 (2015).

28. Fridley, J. D. & Sax, D. F. The imbalance of nature: Revisiting a Darwinian framework for invasion biology. *Glob. Ecol. Biogeogr.* **23,** 1157–1166 (2014).

29. Dyer, E. E., Redding, D. W. & Blackburn, T. M. The global avian invasions atlas, a database of alien bird distributions worldwide. *Sci. Data* **4,** 170041 (2017).

30. Helmus, M. R., Mahler, D. L. & Losos, J. B. Island biogeography of the Anthropocene. *Nature* **513,** 543–546 (2014).

31. Hortal, J., Lobo, J. M. & Jiménez-Valverde, A. Limitations of biodiversity databases: Case study on seed-plant diversity in Tenerife, Canary Islands. *Conserv. Biol.* **21,** 853–863 (2007).

32. Jones, O. R., Purvis, A. & Quicke, D. L. J. Latitudinal gradients in taxonomic overdescription rate affect macroecological inferences using species list data. *Ecography (Cop.).* **35,** 333–340 (2012).

33. Kalwij, J. M. Review of ‘The Plant List, a working list of all plant species’. *J. Veg. Sci.* **23,** 998–1002 (2012).

34. Brummitt, R. K. *World Geographical Scheme for Recording Plant Distributions Edition 2*. (2001). doi:10.1043/0363-6445-28.4.807

35. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25,** 1965–1978 (2005).

36. Klein Goldewijk, K., Beusen, A., Van Drecht, G. & De Vos, M. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* **20,** 73–86 (2011).

37. Gennaioli, N., La Porta, R., Lopez De Silanes, F. & Shleifer, A. Growth in regions. *J. Econ. Growth* **19,** 259–309 (2014).

38. The Worldbank. Dataset: GDP per capita (current US$). *World Bank national accounts data and OECD National Accounts data files* (2015).

39. United Nations Statistics Division. Dataset: Per capita GDP at current prices - US dollars. *National Accounts Estimates of Main Aggregates* (2015).

40. Cody, M. L. *Plants on Islands - Diversity and Dynamics on a Continental Archipelago*. (University of California Press., 2006).

41. Warton, D. I. & Hui, F. K. C. The arcsine is asinine: The analysis of proportions in ecology. *Ecology* **92,** 3–10 (2011).

42. Bates, D., Maechler, M., Bolker, B. M. & Walker, S. Fitting linear mixed-effects models using {lme4}. *J. Stat. Softw.* **67,** 1–48 (2015).

43. Bjornstad, O. N. ncf: Spatial Nonparametric Covariance Functions. R package version 1.1-7. (2016). at <https://cran.r-project.org/package=ncf>

Methods

Global island distribution

The dataset comprises a total of 240 islands and island groups (i.e. archipelagos; hereafter also referred to as islands) of oceanic and continental origin with a minimum size of 5 km². We only included subtropical and tropical islands situated between 30°N and 30°S latitudes. Due to the distribution of landmasses across the globe, there are no remote (i.e. geographically isolated) islands in arctic regions. Temperature and isolation are thus closely correlated and would cause a distortion of the isolation effect.

Datasets

The dataset differed among taxonomic groups, including 109 islands for vascular plants, 89 islands for ants, 129 islands for mammals and 79 islands for reptiles. Species lists of native and established alien species (*sensu* Blackburn [18]) were compiled from various sources (Tab. S6). Large data compilations may be affected by biases in data quality and completeness (i.e. varying sampling strategies, differences in taxonomic concepts; [31,32]). To address these issues, we compiled complete species lists where available based on recent database projects that ensure taxonomic standardization (e.g. using the Plant List for vascular plants; [33]). Furthermore, for all other islands where only richness values were available the most up-to-date sources were used, assuming that these sources used a recent taxonomic concept so that biases can largely be excluded.

Potential effects of variation in data reliability were tested using a sensitivity analysis (see below). Each island was assigned to a geographic region following the Biodiversity Information Standards (TDWG) classification [34] (see Tab. S4). For all islands, we compiled eight predictor variables which represented socio-economic (human population density, per capita gross domestic product), climatic (mean annual temperature, annual precipitation sum) and geographic (island area, elevational range and distance to mainland) variables. Distance to mainland was calculated as the shortest geodesic distance to a continent, excluding Antarctica. The geographical distance is just one metric and ocean currents, winds and the richness of source regions also influence immigration rates for native species [2].However, these additional variables are less relevant for aliens as they are introduced through human transport, and so we decided to use geographical distance only. Island area and elevational ranges were calculated for each island and island group. In the case of island groups the cumulative terrestrial surface area of all relevant islands was used. Island area ranged from 5.11 km^2 to 110,730 km^2, with a median size of 280 km^2. Data on current climate for each region were derived from WorldClim 2.0 [35]). Finally, human population density was derived from the HYDE database [36], and per capita gross domestic product (GDP) from Gennaioli [37], Worldbank [38] and the United Nations [39] (Tab. S5).

Statistical analysis

We analyzed the dependence of alien and native species richness (species numbers) on distance to mainland, island area, elevational range, mean annual temperature, annual precipitation sum, GDP and human population density as predictor variables by means of generalized linear mixed effects models (GLMMs) with a Poisson-distributed response (species richness) and the canonical log link function. Human population density, a frequently used surrogate of human impact (e.g. [13,14]), was never significant and was thus excluded from the analyses. A random effect intercept term with TDWG 4 region as grouping factor acknowledged political/socio-economic groupings among regions, and a random effect intercept term for island geologic setting (i.e. oceanic islands vs. islands situated on continental shelfs [40]) accounted for possible differences in colonization due to historic connections with continents [2]. Finally, an additional observation-level random effect term accounted for overdispersion [41]. To improve symmetry, linearity, and to stabilize variances, numerical predictors were subjected to appropriate transformations (natural log for island area, elevational range, distance to mainland; square root for precipitation sum and per capita GDP), and finally standardized. The magnitude of regression coefficients was hence representative of relative effect size. We fitted individual models for alien, native and total (alien plus native) species numbers for every taxonomic group. Model residuals were assessed for spatial autocorrelation by spline (cross-) correlograms, and no spatial-autocorrelation was found (Fig. S1 & S2).

All statistical analyses were performed using R (version 3.3.1). For GLMM analyses, we used the function *glmer()* from the package lme4 for fitting [42] and the function *effect()* from the package effects for partial effect plots. For spline corellograms, we used the function *spline.correlog()* from the package ncf [43].

Sensitivity analysis

To test the robustness of the assessed relationships between alien species richness and island isolation, we performed a sensitivity analysis. The aim of this analysis was to exclude systematic biases in the data that might stem from heterogeneous sampling intensity or overrepresentation of selected geographical regions, as well as from variable data quality depending on data sources. Therefore, we first systematically excluded islands of a geographic region (based on TDWG level 2 classifications) from the datasets. Then, the number of excluded islands was resampled from the remaining islands to ensure constant sample sizes. Subsequently, we fitted the same GLMMs as were used for the main analysis to the resampled datasets. This procedure was repeated 500 times and confidence intervals were calculated for the regression coefficients and p-values (Table S2). Similarly, we excluded some less reliable data sources, resampled from the remaining islands and recalculated the models.

Acknowledgments:

This study was supported by grants from the Austrian Science Foundation FWF (grant I2096-B16 to DM, BL, FE, SD, TM), the Deutsche Forschungsgemeinschaft (DFG, grant KL 1866/9-1 to MvK and WD, grant SE 1891/2-1 to HS), and grant FZT 118 to iDiv supporting MW. PP and JP were supported by the Czech Science Foundation (project no. 14-36079G, Centre of Excellence PLADIAS), long-term research development project RVO 67985939 (The Czech Academy of Sciences), and by Praemium Academiae award from The Czech Academy of Sciences to PP. EPE was supported by subsidy funding to the Okinawa Institute of Science and Technology, We are indebted to the many colleagues and collaborators who helped us in compiling the native and alien species-data. Pictograms were derived from the PhyloPic website (www.phylopic.org). Image credit for *Platanus occidentalis* L. goes to Michele M Tobias (http://phylopic.org/image/806a6ae9-28a0-4dc6-beeb-f6129a44f10e/). No changes were applied to the pictures. All other images are under no copyright and free to use.

List of supplementary material:

Supporting Information
Table S1 – S6
Fig S1 – S2
References

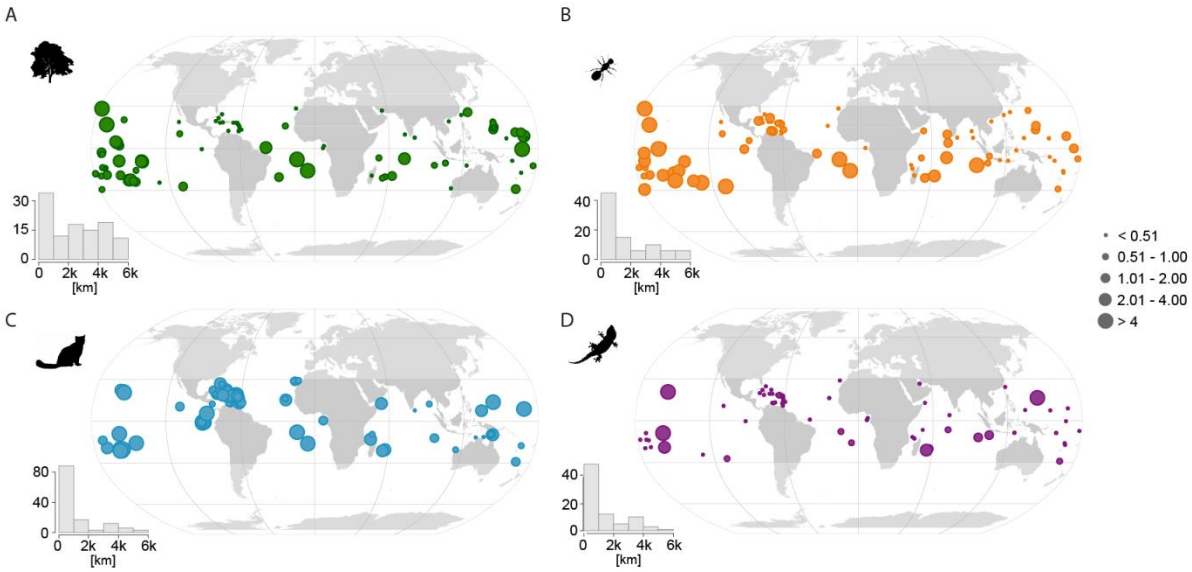

Fig. 1. **Geographic distribution of tropical and subtropical islands used in the study for (A) vascular plants, (B) ants, (C) mammals and (D) reptiles.** Symbol size scales with ratios of established aliens in relation to native species. The histograms show the frequency distributions of island distance to mainland for the four taxonomic groups. The number of islands included in the analysis differs among the taxonomic groups (vascular plants = 109; ants = 89; mammals = 129; reptiles = 79). Pictograms for the taxonomic groups are taken from www.phylopic.org.

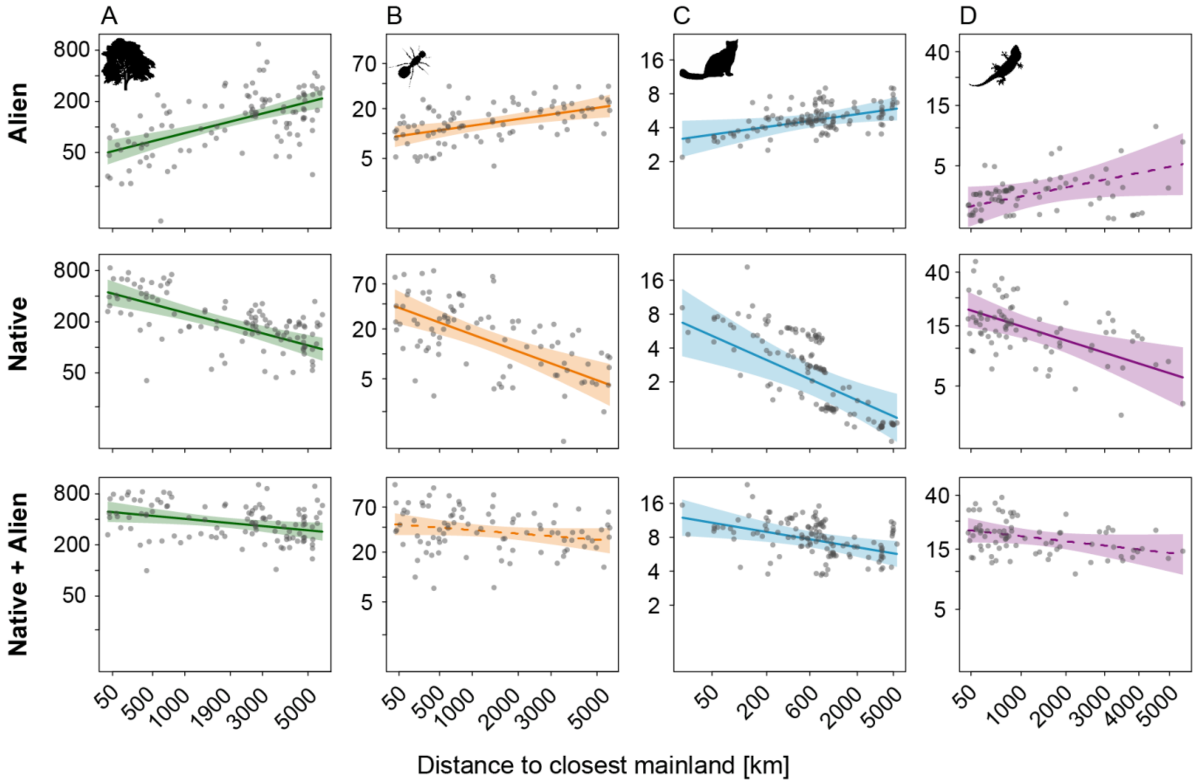

Fig. 2. Alien and native species richness on islands dependent on island isolation for (A) vascular plants, (B) ants, (C) mammals and (D) reptiles. Shown are partial residual plots of the species richness-isolation relationships for established alien (1st row), native (2nd row) and total (3rd row) species richness (log-log space). Generalized linear mixed effects models with a Poisson-distributed response were applied to additionally account for island size, heterogeneity (elevational range) climate (temperature, precipitation) and human impact (per capita GDP). Each column represents one taxonomic group. Shading around the regression line indicates its 95% confidence interval. Dashed lines indicate insignificant results. Pictograms for the taxonomic groups are taken from www.phylopic.org.

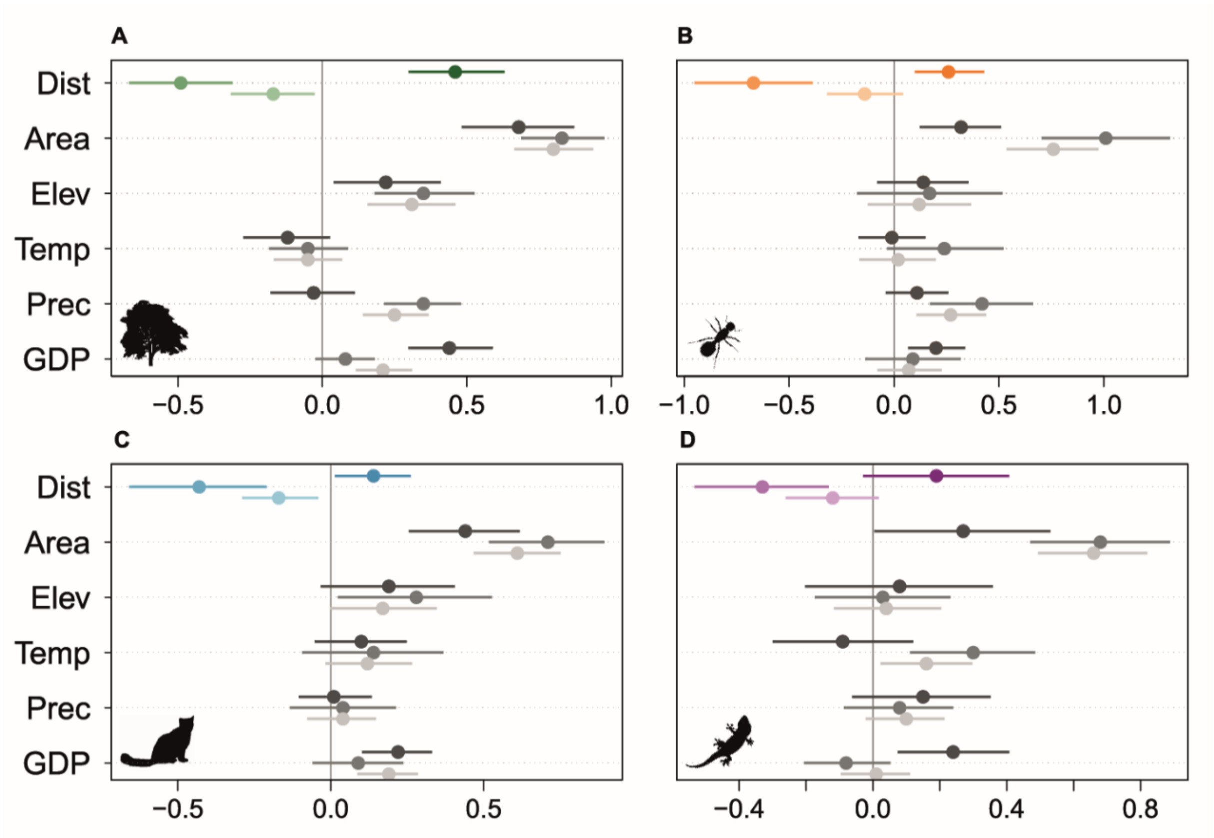

Fig. 3. Regression coefficients and 95% confidence limits for the standardized predictor variables in the generalized linear mixed effects models for (A) vascular plants, (B) ants, (C) mammals and (D) reptiles. Dark colors represent the estimates for established alien species, medium colors for native species and light colors for all species. Abbreviations are: Area: island area; Elev: elevational range; Dist: Distance to the closest mainland; Temp: mean annual temperature; Prec: annual precipitation sum; GDP: per capita GDP (for the full model output see Table S1A). Pictograms for the taxonomic groups are taken from www.phylopic.org.