Journal of Biogeography (J. Biogeogr.) (2015) **42**, 8–10

COMMENTARY

Island floras are not necessarily more species poor than continental ones

Oceanic islands typically exhibit a lower number of species per unit area than continents owing to their geographical isolation (MacArthur & Wilson, 1967). This relationship demonstrates a remarkable consistency across spatial and taxonomic scales (MacArthur & Wilson, 1967) and has significant evolutionary consequences because island organisms are expected to respond to the empty niche space through a series of major transformations in their life-history traits (see Whittaker & Fernández-Palacios, 2007). The biological, ecological and physiological changes are known as island syndromes, with the loss of dispersal power, changes in body size and the development of woodiness in herbaceous plant lineages being some of the most striking examples (Whittaker & Fernández-Palacios, 2007).

In their seminal book, MacArthur & Wilson (1967) observed that the degree of impoverishment in bird faunas distributed across the archipelagos of Melanesia, Micronesia and Polynesia increased from islands near to New Guinea to intermediate and far islands (distance of > 3200 km from the mainland). This implies that the mismatch between species richness per unit area on continents and on islands increases with the degree of isolation of the latter, as species are progressively filtered out depending on their long-distance dispersal capacities (Whittaker & Fernández-Palacios, 2007). However, there is mounting evidence for the existence of lineage-specific species–area relationships associated with long-distance dispersal capacities (Triantis *et al.*, 2012; Patiño *et al.*, 2014b) and this raises the question of whether communities of highly mobile organisms are necessarily less species rich on islands than on continents and, hence, whether they exhibit typical island syndromes.

Here, data from a global survey of 421 land plant floras (Patiño *et al.*, 2014b) were submitted to linear mixed-effects models to analyse variation in log(species richness) depending on log(area) while controlling for variation in the factors geology (continents, oceanic islands and continental islands), plant group (seed plants, ferns and fern allies, liverworts and mosses), biome and realm (the latter two as defined by Olson *et al.*, 2001). The analyses demonstrate that whereas species richness patterns of seed plants conform to the expectations of the island impoverishment theory, spore-producing plants do not (Fig. 1). The species–area models obtained indicate that seed plants exhibit, on average, a continual decrease in species richness per unit area from continents to continental islands to oceanic islands (Fig. 1). Mosses only partially follow such a pattern, with oceanic islands showing the lowest species richness, but with continental regions and continental islands showing similar values for comparable units of area. In liverworts and ferns, the pattern is different. Whereas islands with a small area and presumably limited ecological complexity show impoverished floras, intermediate and large sized oceanic and continental islands display similar or even slightly higher levels of species richness than continents. Thus, oceanic island floras of liverworts and ferns with a log(area) ranging from three to four units (10^3–10^4 km^2), and continental island floras with a log(area) from five to six (10^5–10^6 km^2), exhibit higher species richness compared to continents, a pattern at odds with expectations (Fig. 1).

Possible explanations for the patterns observed in spore-producing land plants are: (1) higher speciation rates on islands than on continents; (2) lower extinction rates on islands; (3) higher dispersal power than in seed plants; or (4) a higher carrying capacity on large islands per unit area than on continents. The generally very low rates of endemism in oceanic island ferns and bryophytes (Patiño *et al.*, 2014a) suggest a lack of extensive island radiations in these groups, thus pointing to the other hypotheses. A global comparison of island and mainland environments revealed that wet climates typical of tropical and, especially, temperate rain forest biomes are over-represented on islands, whereas hot and dry desert climates are under-represented (Weigelt *et al.*, 2013). These general features of islands are particularly suitable for organisms such as bryophytes and ferns that rely greatly on environmental humidity for water uptake (e.g. poikilohydry in filmy ferns and bryophytes) and exhibit lower temperature optima than flowering plants (Vanderpoorten & Goffinet, 2009; Mehltreter *et al.*, 2010). Given the ecological requirements of these spore-producing plant groups with higher dispersal capabilities than in seed plants, such a combination of humidity and mild temperatures on islands could lead to a reduced extinction risk following colonization and a potentially higher carrying capacity than in continental regions of similar area.

The fact that island spore-producing floras are not impoverished suggests that the shifts in the expression of reproductive traits observed in island bryophytes, such as the higher investment in asexual reproduction as well as the higher frequency of fertile shoots (Patiño *et al.*, 2013), do not represent a response to empty niche space, as island biogeography theory predicts. Rather, such changes may reflect a response to the specific climate conditions that prevail on islands. Such environmental conditions may also be found on continents, but proportionally represent a smaller fraction of continental climates (Weigelt *et al.*, 2013) and, hence, the emergence of a bias in life-history traits associated with such climates would not be linked to geographical isolation either. In seed plants, experimental support for the loss of dispersal capacity on islands is equivocal (contrast, e.g. Whittaker & Fernández-Palacios, 2007 and Talavera *et al.*, 2012) and in spore-producing plants, a study on the dispersal capacity of the moss *Rhynchostegium riparioides* failed to demonstrate any significant difference in migration rates in insular and continental populations (Hutsemékers *et al.*, 2011). This raises the question of whether other typical island syndromes,

http://wileyonlinelibrary.com/journal/jbi
doi: 10.1111/jbi.12422

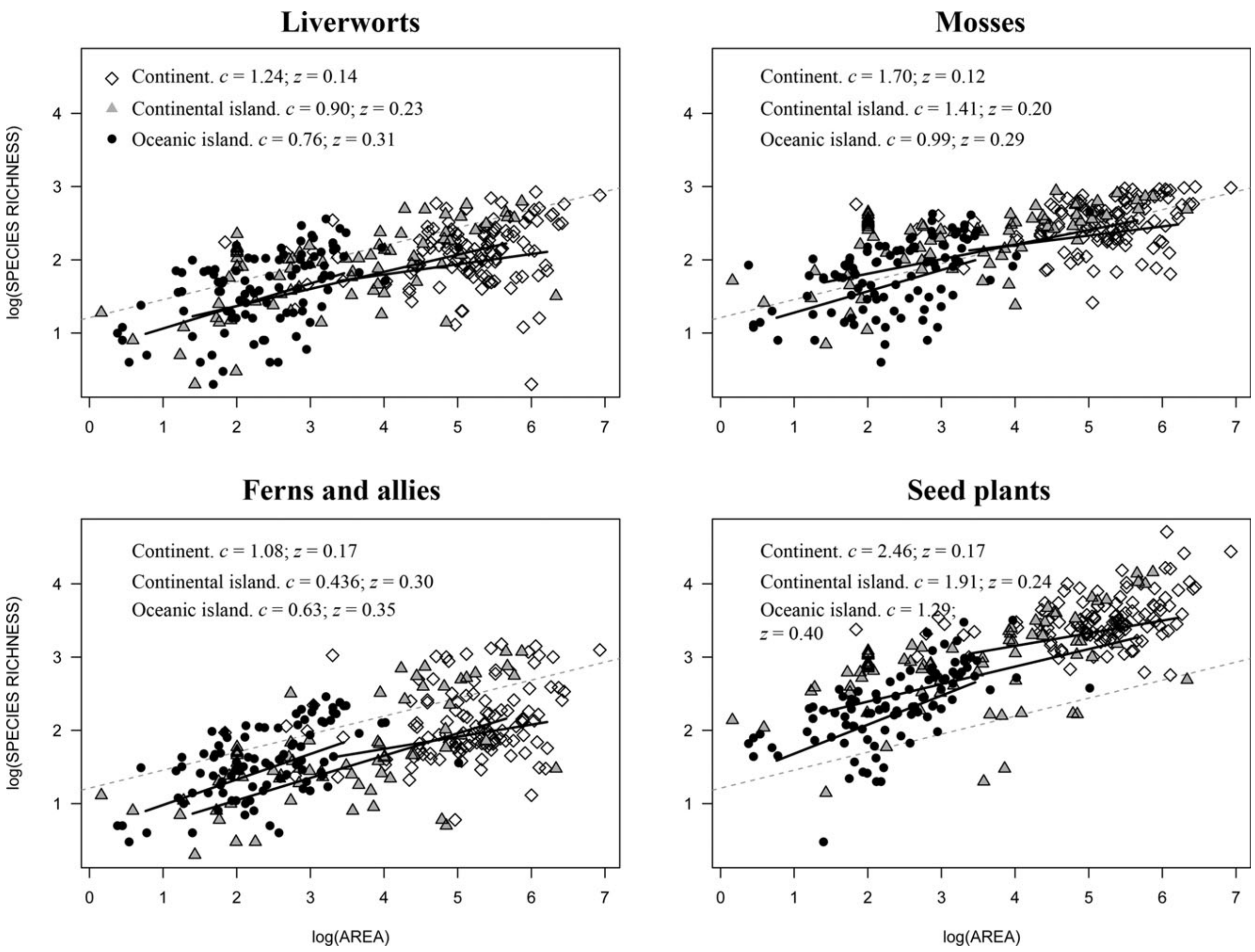

Figure 1 Relationships between log of species richness and log of area (km^2) in continents (n = 123; white rhomboids), continental islands (n = 77; grey triangles) and oceanic islands (n = 97; black circles) for liverworts, mosses, ferns (including fern allies) and seed plants. The regression lines are derived from linear mixed-effects models accounting for variation among geological contexts, lineages of land plants, biomes and realms (for methodological details, see Patiño *et al.*, 2014b). The grey line is the global species–area relationship and the black lines are the species–area relationships per taxon and geology; the lines were fitted using the LME4 R package (Bates *et al.*, 2014). The intercept (c) and slope (z) values for each geological context from the fixed-effects structure of the model are shown.

such as density compensation (e.g. Whittaker & Fernández-Palacios, 2007), which refers to the higher density of a species on an island as a result of the competitive release associated with lower overall species richness, prevail in highly dispersive organisms. Further research to investigate life-history traits associated with departures from the expectations of the island syndrome theory will contribute to the future development of the island biology paradigm.

Jairo Patiño[1,2,3]*,
Péter Sólymos[4],
Mark Carine[5],
Patrick Weigelt[6,7],
Holger Kreft[6],
and Alain Vanderpoorten[1,3]

[1]Department of Biology, Ecology and Evolution, University of Liège, Liège, Belgium, [2]Department of Plant Biology, University of La Laguna, Tenerife, Spain, [3]Azorean Biodiversity Group (GBA, CITA-A) and Platform for Enhancing Ecological Research & Sustainability (PEERS), Universidade dos Açores, Terceira, Portugal, [4]Department of Biological Sciences, Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Canada, [5]Department of Life Sciences, The Natural History Museum, London, UK, [6]Biodiversity, Macroecology and Conservation Biogeography Group, University of Göttingen, Göttingen, Germany, [7]Systemic Conservation Biology, University of Göttingen, Göttingen, Germany

**E-mail: jpatino.llorente@gmail.com*

ACKNOWLEDGEMENTS

The authors greatly valued the constructive insights of two referees. J.P. and A.V. gratefully acknowledge financial support from the Belgian Funds for Scientific Research (FNRS) and the University of Liège. P.W. and H.K. acknowledge support from the German Research Council (DFG) Free Floater Program in the Excellence Initiative at the University of Göttingen and in the scope of the BEFmate project from the Ministry of Science and Culture of Lower Saxony.

REFERENCES

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: linear mixed-*

effects models using Eigen and S4. R package version 1.1-7. Available at: http://cran.r-project.org/web/packages/lme4/index.html.

Hutsemékers, V., Szövényi, P., Shaw, A.J., González-Mancebo, J.-M., Muñoz, J. & Vanderpoorten, A. (2011) Oceanic islands are not sinks of biodiversity in spore-producing plants. *Proceedings of the National Academy of Sciences USA*, **108**, 18989–18994.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Mehltreter, K., Lawrence, R.W. & Joanne, M.S. (2010) *Fern ecology*. Cambridge University Press, Cambridge, UK.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience*, **51**, 933–938.

Patiño, J., Bisang, I., Hedenäs, L., Dirkse, G., Bjarnason, Á.H., Ah-Peng, C. & Vanderpoorten, A. (2013) Baker's law and the island syndromes in bryophytes. *Journal of Ecology*, **101**, 1245–1255.

Patiño, J., Carine, M.A., Fernández-Palacios, J.M., Otto, R., Schaefer, H. & Vanderpoorten, A. (2014a) The anagenetic world of the spore-producing plants. *New Phytologist*, **201**, 305–311.

Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K.A., Naranjo-Cigala, A., Sólymos, P. & Vanderpoorten, A. (2014b) Differences in species–area relationships among the major lineages of land plants: a macroecological perspective. *Global Ecology and Biogeography*, **23**, 1275–1283.

Talavera, M., Arista, M. & Ortiz, P.L. (2012) Evolution of dispersal traits in a biogeographical context: a study using the heterocarpic *Rumex bucephalophorus* as a model. *Journal of Ecology*, **100**, 1194–1203.

Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology and statistics. *Journal of Biogeography*, **39**, 215–231.

Vanderpoorten, A. & Goffinet, B. (2009) *Introduction to bryophytes*. Cambridge University Press, Cambridge, UK.

Weigelt, P., Jetz, W. & Kreft, H. (2013) Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences USA*, **110**, 15307–15312.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford, UK.

Editor: Len N. Gillman