

Domestic exotics and the perception of invasibility

Qinfeng Guo^{1*} and Robert E. Ricklefs²

¹USDA FS, Eastern Forest Environmental Threat Assessment Centre, 200 WT Weaver Blvd., Asheville, NC 28804, USA,

²Department of Biology, University of Missouri-St. Louis, St. Louis, MO 63121, USA

ABSTRACT

Susceptibility of an area to invasion by exotic species is often judged by the fraction of introduced species in the local biota. However, the degree of invasion, particularly in mainland areas, has often been underestimated because of the exclusion of 'domestic exotics' (those introduced to internal units from within the national border) in calculations. Because all introduced species on islands are considered as exotics, this contributes to the perception that islands are more susceptible to invasion than are continental regions. Here, we determine the contribution of domestic exotic species to the degree of invasion (exotic fraction) in mainland areas. We quantify the relationships of exotic fraction to the area, human population density and land use within each of the 48 conterminous US states to identify mechanisms that potentially influence the degree of invasion. For each of the 48 conterminous US states, we compiled the number of species introduced from outside the United States ('foreign exotics') and the number of exotics introduced from other conterminous US states ('domestic exotics'). The status of each species as foreign or domestic was determined for each state by researching its precise origins through vouchered herbarium records, supplemented by literature (Kartesz, 2010). We found that (1) the exotic fraction inevitably decreases with increasing area as the pool of potential exotic species decreases; (2) exotic richness of areas within large mainland regions is underestimated to the extent that species introduced among areas within a region are considered as natives; and (3) human activities contribute disproportionately more exotics to smaller than to larger administrative areas. How we define 'exotic' influences how we count non-native species and perceive invasibility. Excluding domestic exotics in mainland regions leads to a biased perception of increased invasibility on islands, where all introduced species are considered exotic. Thus, future documentation and interpretation of invasion patterns and management of exotics should account for these biases in quantifying the exotic fraction.

Keywords

Area, biological invasions, definition of exotic, degree of invasion (DI), diversity, homogenization, islands, population, scale-dependency.

*Correspondence: Qinfeng Guo, USDA FS, Eastern Forest Environmental Threat Assessment Centre, 200 WT Weaver Blvd., Asheville, NC 28804, USA.
E-mail: qguo@fs.fed.us

INTRODUCTION

The proportion of exotic species (the exotic fraction) on islands has been reported to be almost three times that of mainland sites of similar size (Lonsdale, 1999). The disproportionately larger fraction of exotic species has been cited as indicating that islands are highly vulnerable to invasion (Elton, 1958; but see Bellemain & Ricklefs, 2008). Although the generality of this claim has been questioned (e.g.

D'Antonio & Dudley, 1995; Lonsdale, 1999; Sol, 2000), this perception persists in the literature on biotic invasions. Here, we revisit the definition of 'exotic species' and the associated boundaries delimiting areas of concern, and propose two additional explanations for the higher exotic fractions and perceived higher invasibility, of smaller regions, including islands. First, with smaller area, particularly combined with the discrete boundaries of islands, more species are 'external' and thus represent potential invaders relative to the num-

ber of natives. Species introduced to mainland areas from within the larger geographic region are less likely to be considered exotics. Second, the greater density of human populations within smaller regions, including islands, increases the pressure of introductions (e.g. Lockwood *et al.*, 2009).

We define exotic species, variously called introduced, alien, non-indigenous or non-native species, as species living outside their native distributional ranges because of human activity, either deliberate or accidental (e.g. Williamson, 1996; Richardson *et al.*, 2000; Pyšek *et al.*, 2004). Yet, common practice and the general public perception in counting exotic species often do not match this generally accepted definition (Chown *et al.*, 1998; Lonsdale, 1999). The exotic species within a circumscribed area should include all the species whose native ranges lie outside the area, even when they occur within the same geographic region or continent (Pyšek *et al.*, 2004). Because islands tend to have fewer native species than comparable continental areas, the exotic fraction and the invasibility of island ecosystems also typically appear to be higher.

Non-native species on islands can be distinguished readily from natives because islands have unambiguous boundaries. Within continental regions, the definition of exotic species is, in many cases, less straightforward (Pyšek *et al.*, 2004). In particular, species that are exotic to an area of concern but which occur naturally in the surrounding region are often considered as native. Within the conterminous United States, the numbers of native and exotic species in states or counties are based on the status of species as native or exotic in the entire country (or even the whole of North America; e.g. USDA & NRCS, 2004), not to the states or counties themselves. In contrast, every species introduced to Hawaii is defined as an exotic, including species native to the United States or North America. Using Hawaii's own border to define exotics offers a more realistic assessment of the exotic species fraction (but not necessarily invasibility, which is an inherent property of an ecosystem; see Lonsdale, 1999).

Because internal (or in-country, e.g. state-to-state) species introductions have not been closely monitored, the exact number of domestic species introductions among US states (the so-called homegrown exotics; Cox, 1999) is difficult to obtain (but see Fuller *et al.*, 1999 for fishes and Kartesz, 2010 for plants). For example, Fuller *et al.* (1999) reported that 60% of introduced fish species in river drainages of the United States are native to the United States (in other drainages), but only 36% are from foreign countries and considered exotics. In the New Mexico flora, between 1915 and 2000, exotics from outside North America increased 2.7-fold from 128 to 346, while the exotics introduced from other parts of North America (i.e. the portion missing in quantifying exotic richness for almost all other states by current practice) increased more rapidly (5.5-fold, from 8 to 44) (Cox, 2001). This problem of domestic exotics has previously been recognized (e.g. Cox, 1999; Palmer, 2005; Qian &

Ricklefs, 2006), but its severity and potential impacts on many aspects of invasion ecology have received little attention.

Here, using a new comprehensive compilation of data on plant distributions in the 48 conterminous US states, we determine the degree to which domestic exotic species contribute to the exotic fraction (or degree of invasion). We also quantify the statistical relationship of exotic fraction to state area, human population density and land use within each state to identify mechanisms that potentially influence the exotic fraction.

METHODS

Because different habitats naturally support different numbers of species, invasibility is often measured relative to native diversity, and the exotic fraction is taken as the degree of invasion (DI; Lonsdale, 1999; Guo & Symstad, 2008). From the standpoint of assessing invasibility, one might instead quantify established exotic species relative to the total number of introductions, but this quantity is more difficult to ascertain (see, however, Blackburn *et al.*, 2008).

For each of the 48 conterminous US states, we compiled the number of species introduced from outside the United States (foreign exotics) and those introduced to states from within the country (domestic exotics). Numbers of exotics were obtained for each state from Kartesz & Meacham (1999) and USDA & NRCS (2004). Their status as foreign or domestic was determined for each state by researching their precise origins through vouchered herbarium records, supplemented by literature (for more details, see Kartesz, 2010).

RESULTS AND DISCUSSION

Exotic fractions are clearly higher in smaller than in larger states within the United States (Fig. 1a), partly because native species richness increases with area but the number of exotics bears no consistent relationship to the size of a state (i.e. exotic floras are more homogenized than native floras, see Qian & Ricklefs, 2006; but also see Blackburn *et al.*, 2008; Fig. 1b). Moreover, domestic exotics inflate the exotic fraction more in smaller than in larger states (Fig. 1a). In continental areas, using a larger external boundary to estimate exotic richness in smaller, internal units leads to increasing bias with progressively smaller area (Fig. 2). Comparable data for islands are less likely to suffer this bias because all introduced species typically are considered exotic.

How we define exotics also influences the relationship between exotic and native species. For example, exotic species richness based on each states' own boundary is not significantly related to native species richness ($r^2 = 0.04$, $P > 0.05$), although previous analyses using the US border to define exotics (and with Hawaii and Alaska included) reported significant positive correlations ($r^2 = 0.11$, $P < 0.05$; e.g. Fridley *et al.*, 2004).

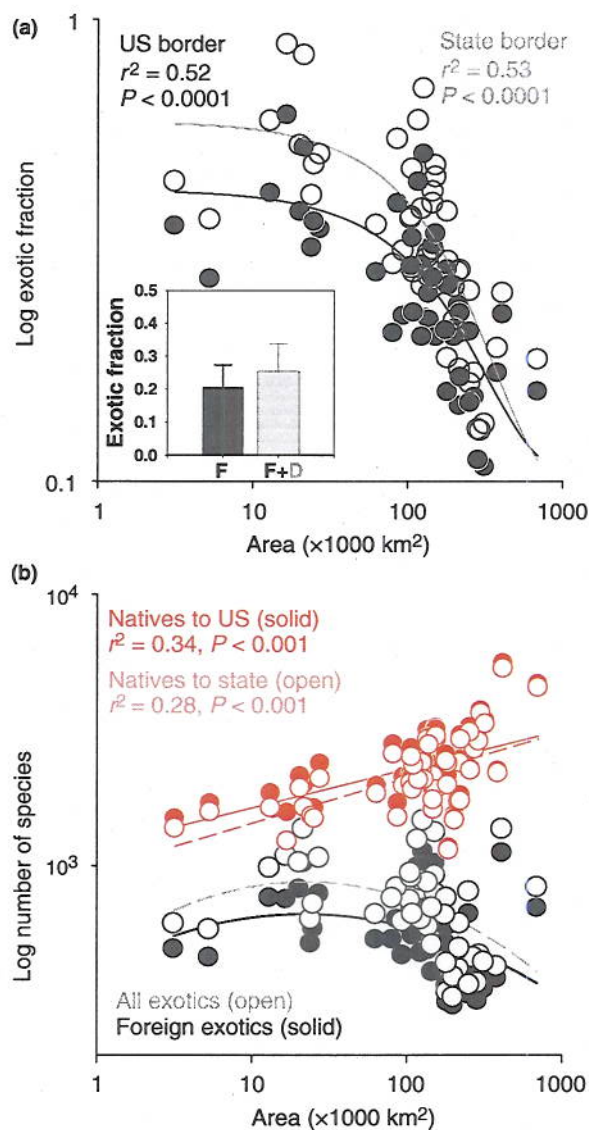


Figure 1 The relative contributions of foreign and domestic exotic species to each of the 48 conterminous US states. Top: Decline of the exotic fraction (0–1) with area (log–log scale). The numbers of vascular plant species exotic and native to the entire USA in each state (solid) are from Kartesz & Meacham (1999) and USDA & NRCS (2004), and those exotic or native to each US state (open) are from Kartesz (2010). The inserted panel shows the difference between the traditional and new measures of exotic fraction (F = foreign exotics introduced to the US and D = domestic exotics introduced from other US states). Bottom: The species–area relationships (log–log scale) for both native and exotic plants when both the whole US and each state’s border were used (i.e. domestic exotics were either excluded or included).

Smaller political units, including islands, support higher human population densities than larger units (e.g. Crawley, 1987; Brown, 1989; Rejmánek, 2003), which contributes to their higher exotic/native ratios (Fig. 3). Indeed, islands in general suffer greater human influence, including greater propagule pressure (D’Antonio & Dudley, 1995; Rejmánek,

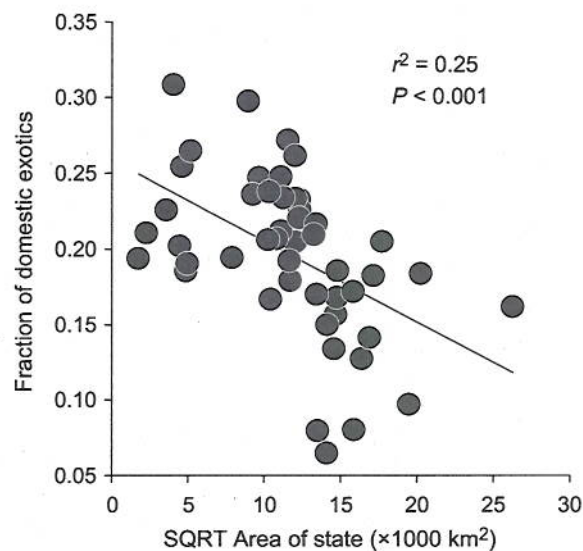


Figure 2 The fraction of domestic exotic plants in the total ‘exotic’ flora in each of the 48 conterminous continental US states and its relationship with the area of state. The area was square-root transformed so that it is approximately proportional to the length of the state boundary. Using states perimeter data yielded similar results but the results could vary widely with spatial scales.

1996; Duncan *et al.*, 2003; Blackburn *et al.*, 2008). The overwhelming force of human introduction of exotics overrides the effect of isolation on species immigration, a unique feature of island systems (Blackburn *et al.*, 2004; Gimeno *et al.*, 2006; Bellemain & Ricklefs, 2008). In addition, because species richness on remote islands is limited by long-distance dispersal, islands tend to hold few native species and the exotic fraction consequently is inflated relative to continental areas with similar numbers of exotic species. Because of this, invasion success and the invasibility of islands should be judged by the proportion of successful introductions rather than the number of established exotic species.

Although intercontinental species introductions capture our attention, internal or near-distance introductions (i.e. from other states or counties, depending on the reference area) continue at a high rate owing to proximity, environmental similarity and facilitation of both intentional and unintentional introductions associated with increasing human activities across state and national borders within continents. Distinguishing species introduced across state or provincial borders from ‘natural’ migrants (not ‘exotics’ by definition) can be difficult, particularly for ecosystems within which plants might disperse across geopolitical boundaries. The monitoring of species introductions across national borders and internal state borders also is strongly biased with respect to taxonomic group (e.g. plants are less well tracked than fishes; Fuller *et al.*, 1999).

Our data and analyses support the increasing number of authors, including Simberloff (1995) and Sol (2000), who have

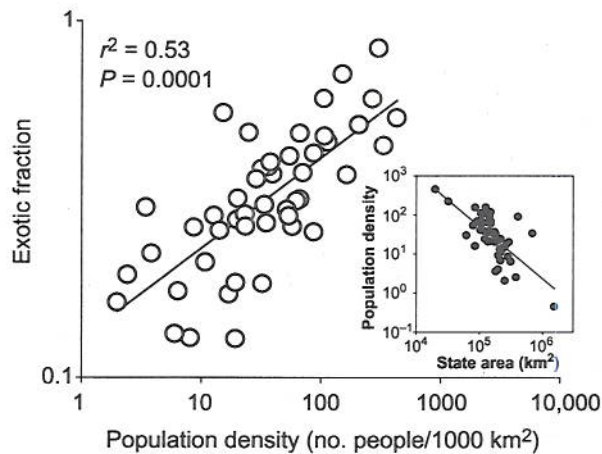


Figure 3 The positive relationship between human population density (individuals per km²) and the exotic fraction (foreign and domestic) in the 48 conterminous US states (each dot represents a state; data for all countries worldwide showed the same trend ($r^2 = 0.31$, $P < 0.0001$). Although larger geopolitical units (e.g. states) have greater human population sizes, smaller units usually have higher population densities (the inserted panel; $r^2 = 0.49$, $P < 0.001$). The positive correlation between human population size and exotic richness has recently been suggested as an area effect (e.g. Rejmánek, 2003). However, data from the 48 conterminous US states show that smaller administrative units also have greater human population densities, which could contribute more exotic richness in smaller units than in larger units. Data are from the U.S. Census Bureau, Population Division. 2009. National and State Population Estimates – Annual Estimates of the Resident Population for the United States, Regions, States, and Puerto Rico: April 1, 2000 to July 1, 2009 (NST-EST2009-01).

challenged the dogma on island invasibility (see also D'Antonio & Dudley, 1995; Li *et al.*, 2006; Jeschke, 2008). When the relative establishment rates and actual introduction rates of various types of organisms are taken into account, these authors show that invasion success rate (or invasibility, i.e. proportion of introductions becoming established or invasive, in contrast to exotic fraction or degree of invasion), is not necessarily higher on islands and it is unrelated to the size of islands or continents, in contrast to the exotic fraction.

In addition to challenging earlier statements about island invasibility, our analysis also calls for caution in interpreting results of comparative studies of invasibility among regions or environments where invasibility or degree of invasion is measured differently, especially where domestic exotics are either included or excluded. Conclusions drawn from such comparisons likely will vary depending on the criteria used to distinguish native and non-native species.

At the state level within the United States, domestically introduced plants account for at least 25% of all exotic species. Internal species introductions also tend to homogenize local, state and national floras (see Qian & Ricklefs, 2006 regarding a similar role of foreign exotics). Domestic species

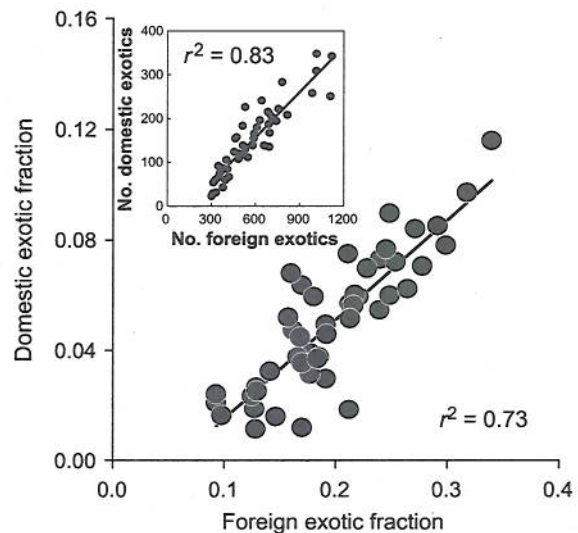


Figure 4 The relationships between foreign and domestic exotic fractions and between foreign and domestic exotic species richness (inserted panel) in the 48 conterminous US states. For both regressions, $P < 0.0001$.

introductions, whether resulting from market-based trade or accident, should be minimized, especially if potential invasiveness has not been fully evaluated (Cox, 1999). Domestic and foreign exotics exhibit similar patterns of richness and exotic fraction among the 48 conterminous states in the United States (Fig. 4; see also Fig. S1), although domestic species constitute a higher fraction of exotics in the smaller states (Fig. 2). Monitoring internal species introductions is difficult; however, given their magnitude and impacts, future policy and management plans should account for domestic introductions. Re-evaluating how we define and perceive exotic species in the future should produce refinements in invasion biology, conservation and biogeography within continental regions.

ACKNOWLEDGEMENTS

We thank J.H. Brown, M. Davis, J. Falcone, D. Hooper, S. Norman, M. Palmer, M. Rejmánek and D.M. Richardson for insightful comments on the manuscript; S. Creed, J. Kartesz, R. Moe, M. Nishino for their help with data compilation; and J. Wen for assistance in statistical analyses. R.E.R. thanks the Curators of the University of Missouri and the Alexander von Humboldt Foundation for support.

REFERENCES

- Belleman, E. & Ricklefs, R.E. (2008) Are islands the end of the colonization road? *Trends in Ecology & Evolution*, **23**, 461–468.
- Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305**, 1955–1958.

- Blackburn, T.M., Cassey, P. & Lockwood, J.L. (2008) The island biogeography of exotic bird species. *Global Ecology and Biogeography*, **17**, 246–251.
- Brown, J.H. (1989) Patterns, modes and extents of invasions by vertebrates. *Ecology of biological invasions: a global perspective* (ed. by J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F. Kruger, M. Rejmánek and M. Williamson), pp. 85–109. John Wiley, New York.
- Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. (1998) Ecological biogeography of Southern Ocean Islands: species–area relationships, human impacts, and conservation. *American Naturalist*, **152**, 562–575.
- Cox, G.W. (1999) *Alien species in North America and Hawaii*. Island Press, Washington, D.C.
- Cox, G.W. (2001) An inventory and analysis of the alien plant flora of New Mexico. *The New Mexico Botanist*, **17**, 1–8.
- Crawley, M.J. (1987) What makes a community invulnerable? *Colonization, succession and stability* (ed. by A.J. Gray, M.J. Crawley and P.J. Edwards), pp. 429–453. Blackwell Scientific, Oxford, UK.
- D’Antonio, C.M. & Dudley, T.L. (1995) Biological invasions as agents of change in islands vs. mainlands. *Biological diversity and ecosystem function* (ed. by P.M. Vitousek, L.L. Loope and H. Adersen), pp. 103–121. Springer, Berlin.
- Duncan, R.P., Blackburn, T.M. & Sol, D. (2003) The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 71–98.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Fridley, J.D., Brown, R.L. & Bruno, J.F. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, **85**, 3215–3222.
- Fuller, P.L., Nico, L.G. & Williams, J.D. (1999) *Nonindigenous fishes introduced into inland waters of the United States*. US Geological Survey, Bethesda, Maryland.
- Jimeno, I., Vilà, M. & Hulme, P.E. (2006) Are islands more susceptible to plant invasion than continents? A test using *Oxalis pes-caprae* L. in the western Mediterranean *Journal of Biogeography*, **33**, 1559–1565.
- Guo, Q. & Symstad, A. (2008) A two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology*, **22**, 666–672.
- Jeschke, J.M. (2008) Across islands and continents, mammals are more successful invaders than birds. *Diversity and Distributions*, **14**, 913–916.
- Kartesz, J.T. (2010) A synonymized checklist and atlas with biological attributes for the vascular flora of the United States, Canada, and Greenland. *Floristic synthesis of North America*, 2nd edn. CD-ROM version 2.0. (ed. by J.T. Kartesz). North Carolina Botanical Garden, Chapel Hill.
- Kartesz, J.T. & Meacham, C.A. (eds) (1999) *Synthesis of the North American flora. CD-ROM version 1.0*. North Carolina Botanical Garden, Chapel Hill.
- Li, Y., Wu, Z. & Duncan, R.P. (2006) Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China. *Oecologia*, **148**, 129–136.
- Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions*, **15**, 904–910.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Palmer, M.W. (2005) Temporal trends of exotic species richness in North American floras: an overview. *Ecoscience*, **12**, 386–390.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.
- Qian, H. & Ricklefs, R.E. (2006) The role of exotic species in homogenizing the North American flora. *Ecology Letters*, **9**, 1293–1298.
- Rejmánek, M. (1996) Species richness and resistance to invasions. *Biodiversity and ecosystem processes in tropical forests* (ed. by G.H. Orians, R. Dirzo and J.H. Cushman), pp. 153–172. Springer-Verlag, Berlin.
- Rejmánek, M. (2003) The rich get richer – responses. *Frontiers of Ecology and the Environment*, **1**, 123–123.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science*, **49**, 87–97.
- Sol, D. (2000) Are islands more susceptible to be invaded than continents? Birds say no *Ecography*, **23**, 687–692.
- USDA & NRCS. (2004) *The plants database version 3.5* (<http://plants.usda.gov>). National Plant Data Centre, Baton Rouge, Louisiana.
- Williamson, M.H. (1996) *Biological Invasions*. Chapman & Hall, London.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 The fraction of all exotic plants in each of the 48 conterminous US states and in seven major regions. Domestic and foreign exotics show similar patterns (see Fig. 4) and thus not shown here separately.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Qinfeng Guo has broad interests in community ecology and biogeography. He is currently working on biodiversity patterns at various scales that may affect the process and patterns of biotic invasions and ecosystem functions. He also studies how life history traits and genetics may influence species invasiveness and how history and habitat characteristics may affect invasibility.

Robert E. Ricklefs is Curators' Professor of Biology at the University of Missouri at St. Louis. His interests include island biogeography, particularly of birds in the West Indies, and the generation and maintenance of patterns of species richness more generally. Much of his work has concerned the influence of large-scale processes, which determine regional species richness, on the diversity of local assemblages of species.

Editor: David Richardson