COMMENT

Origin matters

Van der Wal et al. (2015) (henceforth VdW) attempted to evaluate the degree to which the geographical origin of a species shapes people's attitudes towards conservation management decisions. Based on questionnaire surveys of the general public and experts from Scotland and Canada, the authors perceive "widespread use of the label 'nonnative' as a proxy for harmfulness" and a species' origin as being used as shorthand for "harmfulness" (pp. 349 & 352). However, the authors cited by VdW do not take such a categorical view. All invasion biologists would agree with VdW that the origin of a species should not be the sole criterion for management options, and whether this criterion should be used at all depends on the stages of a non-native taxon along the introduction-naturalization-invasion-impact continuum (Richardson et al. 2000). Once a non-native taxon is introduced and naturalized for a long time without economic or environmental impact, few biologists would cite its origin as a reason to attempt to control or eradicate it, and its removal could inimically affect certain native species. Furthermore, the resources for managing undesirable taxa are always limited, and impact is usually assessed for prioritization. Invasions of non-native species are also often just symptoms, not causes of human-created environmental changes. VdW focus on wellknown species with long introduction histories for which the potential abundance and impact can plausibly be judged by experts and the public alike. However, when a decision is to be made regarding whether a non-native taxon that is not yet present in the local biota should be introduced, or whether a recently established and geographically restricted but spreading non-native taxon should be controlled, the taxon's origin should be a primary component in the decisionmaking process.

For several reasons, non-native taxa are more likely to cause larger economic and/or environmental impacts than taxa that are native to the area of interest. Reasons for this have already been enumerated by Leopold (1942), Paolucci *et al.* (2013) and Simberloff *et al.* (2012), among others. One important reason for taking the origin of the introduced or potentially introduced taxon seriously is the fact that such taxa are not a random sample from the available non-native pools. Lonsdale (1994) demonstrated that the probability of a useful introduced pasture species becoming a weed in Northern Australia was 81% (17 out of 21 species). This trend may even accelerate as new pasture taxa are bred with characteristics that are typical of invasive species and environmental weeds (Driscoll *et al.* 2014). Introduced non-native taxa of pasture plants are non-

random samples with attributes making them more likely to become successful weeds. The same is true of many of the fast-growing tree taxa that have been widely introduced to forest plantations. Species introduced for erosion control and riverbank stabilization (Ammophila arenaria, Carpobrotus spp., Salix spp. and Tamarix spp.) are not a random sample from their respective autochthonous floras. Many ornamental plants are introduced because of showy fruits that are therefore preferably dispersed by birds (Richardson & Rejmánek 2011), or have big and showy flowers that, in general, tend to affect the visitation and reproduction of natives negatively (Morales & Traveset 2009). Introduced fish species are not a random sample from original faunas, but rather consist of those that are desirable to humans and are preferred for their fast growth and reproduction (Moyle & Marchetti 2006; P. Moyle, personal communication 2016). Human commensals are also more frequently introduced, usually to human-altered environments to which they are adapted (Jeschke & Strayer 2008; Buckley & Catford 2016). Nonrandom selection of introduced taxa makes them very often promising candidates a priori for successful and influential invasion.

Species pools themselves are not unbiased. There is a larger probability that non-native species will be introduced from large species pools (e.g. more likely from continents than from islands). An inevitable consequence of these origins is that such species have been exposed to many more interspecific interactions during their recent evolution and therefore are less 'naïve' and potentially more aggressive. For example, in African savannas, the largest species pool of tropical C4 grasses provided species that were adapted to droughts, grazing and fire; many African grasses are highly invasive ecosystem transformers in tropical and subtropical habitats (D'Antonio & Vitousek 1992; Foxcroft et al. 2010). A recent argument is that terrestrial and aquatic regions of higher phylogenetic diversity are more likely to be sources of invasive and competitive species (Fridley & Sax 2014). Many non-native species may have significant impacts on the native biota because of their independent evolutionary histories. In their native range, resident species have coevolved with such native biota and thus have traits permitting their coexistence. The success of non-natives may result from their release from enemies (competitors, pathogens and herbivores), the evolution of increased competitive ability and the more pronounced effects of allelopathy in new environments (Callaway et al. 2008; Hill & Kotanen 2009; Sun et al. 2015). Buckley and Catford (2016) recently summarized such possibilities.

A conclusive piece of evidence that the geographical origin of species matters is the NutNet global grassland experiment across 13 countries, where non-native species were six times more likely to have a maximum cover of at least 80% relative to natives (Seabloom *et al.* 2015). Origin clearly affected local abundance. The NutNet experiment also showed that one native species was lost every 2 years in fertilized plots, while non-native species richness did not change. In general, relative species richness and cover of non-natives increased in fertilized plots.

Non-native herbaceous species may not only benefit more strongly from arriving early than do native species (priority effects) (Wilsey *et al.* 2015), but even their late arrival may come at a lower cost compared to native species (Stuble & Souza 2016). The same species may have more negative impacts in areas of introduction compared with their native range (Hejda *et al.* 2016; Taylor *et al.* 2016). Non-native freshwater species comprise 60% of aquatic pests in North America and Europe and are six times more likely to be pests than native species (Hassan & Ricciardi 2014).

Public perception and involvement are often essential to successful eradication or control programmes (Novoa et al. 2016). Whether public perception of management priorities and the statements of some ecologists agree is an interesting and, in many situations, an important question, as VdW investigated. However, the public may be wrong, and so may be some ecologists. The data and logical inferences presented in the studies mentioned above speak for themselves to ecologists, but they may require explication to the lay public, and it behooves ecologists to present arguments in a clear form to the wider community. Clearly, a precautionary approach to non-native taxa must be recommended. The statistics are very simple: with an increasing number of introduced species, the number of naturalized species increases (Hulme 2012, Fig. 2); and with an increasing number of naturalized species, the number of potentially harmful species also increases (Rejmánek & Randall 2004, Fig. 1; Ricciardi & Kipp 2008, Fig. 2 & 3). Some native species are expanding their range, abundance and impacts on other native taxa (Lima et al. 2012; Simberloff et al. 2012); however, once a non-native taxon is introduced, becomes widespread and its negative environmental and/or economic impacts are recognized, eradication is much more difficult, if even possible with current technology, and control is much more expensive (Rejmánek & Pitcairn 2002; Russell & Broome 2016).

ACKNOWLEDGMENTS

We thank Bethany Bradley and one anonymous referee for helpful comments on the manuscript.

References

Buckley, Y.M. & Catford, J. (2016) Does the biogeographic origin of species matter? *Journal of Ecology* 104: 4–17.

- Callaway, R.M., Cipollini, D., Barto, K., Thelen, G.C., Hallett, S.G., Pati, D. *et al.* (2008) Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. *Ecology* 89: 1043–1055.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63–87.
- Driscoll, D.A., Catford, J.A., Barney, J.N., Hulme, P.E., Inderjit, Martin, T.G. et al. (2014) New pasture plants intensify invasive species risk. Proceedings of the National Academy of Sciences of the United States of America 111: 16622–16627.
- Foxcroft, L.R., Richardson, D.M., Rejmánek, M. & Pysek, P. (2010) Alien plant invasions in tropical and sub-tropical savannas. *Biological Invasions* 12: 3913–3933.
- Fridley, J.D. & Sax, D.F. (2014) The imbalance of nature: revisiting a Darwinian framework for invasion biology. *Global Ecology and Biogeography* 23: 1157–1166.
- Hassan, A. & Ricciardi, A. (2014) Are non-native species more likely to become pests? *Frontiers of Ecology and Environment* 12: 218–223.
- Hejda, M., Štajerová, K. & Pyšek, P. (2016) Dominance has a biogeographical component. *Journal of Biogeography* (DOI: 10.1111/jbi.12801).
- Hill, S.B. & Kotanen, P.M. (2009) Evidence that phylogenetically novel non-indigenous plants experience less herbivory. *Oecologia* 161: 581–590.
- Hulme, P.E. (2012) Weed risk assessment: a way forward or a waste of time? *Journal of Applied Ecology* **49**: 10–19.
- Jeschke, J.M. & Strayer, D.L. (2008) Are threat status and invasion success two sides of the same coin? *Ecography* 31: 124–130.
- Leopold, A. (1942, 1999). Biotic land-use. In: Aldo Leopold. For the Health of the Land. Previously Unpublished Essays and Other Writings, eds. J.B. Callicott & E.T. Freyfogle, pp. 198–207. Washington, DC, USA: Island Press.
- Lima, R.A.F., Rother, D.C., Muler, A.E., Lepsch, I.F. & Rodrigues, R.R. (2012) Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot. *Biological Conservation* 147: 32–39.
- Lonsdale, W.M. (1994) Inviting trouble: introduced pasture species in northern Australia. *Australian Journal of Ecology* 19: 345–354.
- Morales, C.L. & Traveset, A. (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters* 12: 716–728.
- Moyle, P.B. & Marchetti, M.P. (2006) Predicting invasion success: freshwater fishes in California as a model. *BioScience* 56: 515–524.
- Novoa, A., Kaplan, H., Wilson, J.R.U. & Richardson, D.M. (2016) Resolving a prickly situation: involving stakeholders in invasive cactus management in South Africa. *Environmental Management* 57: 998–1008.
- Paolucci, E.M., MacIsaac, H.J. & Ricciardi, A. (2013) Origin matters: alien consumers inflict greater damage on prey populations than do native consumers. *Diversity and Distributions* 19: 988–995.
- Rejmánek, M. & Pitcairn, M.J. (2002) When is eradication of exotic pest plants a realistic goal? In: *Turning the Tide: The Eradication* of Invasive Species, eds. C.R. Veitch & M.N. Clout, pp. 249–253. Gland, Switzerland, and Cambridge, UK: IUCN.
- Rejmánek, M. & Randall, J.M. (2004) The total number of naturalized species can be a reliable predictor of the number of alien pest species. *Diversity and Distributions* 10: 367–369.
- Ricciardi, A. & Kipp, R. (2008) Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions* 14: 374–380.

- Richardson, D.M. & Rejmánek, M. (2011) Trees and shrubs as invasive alien species – a global review. *Diversity and Distributions* 17: 788–809.
- Russell, J.C. & Broome, K.G. (2016) Fifty years of rodent eradication in New Zealand: another decade of advances. *New Zealand Journal* of Ecology 40: 197–204.
- Seabloom, E.W., Borer, E.T., Buckley, Y.M., Cleland, E.E., Davies, K.F., Fim, J. *et al.* (2015) Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications* 6: 7710.
- Simberloff, D., Souza, L., Nunez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology* 93: 598–607.
- Stuble, K.L. & Souza, L. (2016) Priority effects: natives, but not exotics, pay to arrive late. *Journal of Ecology* (DOI: 10.1111/1365-2745.12583).
- Sun, Y., Müller-Schärer, H., Maron, J.L. & Schaffner, U. (2015) Biogeographic effects on early establishment of an invasive alien plant. *American Journal of Botany* 102: 621–625.

- Taylor, K.T., Maxwell, B.D., Pauchard, A., Nunez, A. & Rew, L. (2016) Native versus non-native invasions: biodiversity impacts of *Pinus contorta* in introduced and native ranges. *Diversity and Distributions* 22: 578–588.
- Van der Wal, R., Fischer, A., Selge, S. & Larson, B.M.H. (2015) Neither the public nor experts judge species primarily on their origins. *Environmental Conservation* 42: 349–355.
- Wilsey, B.J., Barber, K. & Martin, L.M. (2015) Exotic grassland species have stronger priority effects than natives regardless of whether they are cultivated or wild genotypes. *New Phytologist* 205: 928–937.

MARCEL REJMÁNEK^{1*} AND DANIEL SIMBERLOFF² ¹Department of Evolution and Ecology, University of California, Davis, California 95616, USA and ²Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996, USA

*Correspondence: Professor Marcel Rejmánek Tel: +1 530 752 1092 e-mail: mrejmanek@ucdavis.edu