

- 3 Reichard, S.H. and Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* 11, 193–203
- 4 Roy, J. *et al.* (1991) Invasion by annual brome grasses: a case study challenging the homocline approach to invasions. In *Biogeography of Mediterranean Invasions* (Groves, R.H. and Di Castri, F., eds), pp. 207–224, Cambridge University Press
- 5 Rejmánek, M. (1999) Invasive plant species and invulnerable ecosystems. In *Invasive Species and Biodiversity Management* (Sandlund, O.T. *et al.*, eds), pp. 79–102, Kluwer Academic Publishers
- 6 Milberg, P. (1999) Survival and growth of native and exotic composites in response to a nutrient gradient. *Plant Ecol.* 145, 125–132
- 7 Sack, L. and Grubb, P.J. (2001) Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? *Funct. Ecol.* 15, 145–154
- 8 Groves, R.H. *et al.*, eds (2001) *Weed Risk Assessment*, CSIRO Publishing

Predicting invaders

Response from Kolar and Lodge

In our recent review in *TREE*¹, we identified trends emerging in the literature between species characteristics and the predisposition of becoming an invader. Given that some ecologists have expressed skepticism about the utility of looking for such characteristics², we are heartened that the comments from Sol³, Gerlach⁴, Rejmánek and Reichard⁵ do not question the usefulness of this approach.

We thank the respondents for identifying our mistakes and omissions. We erroneously indicated that O'Connor⁶ found a significant relationship between bird migration and establishment when, in fact, he did not. In addition, we failed to highlight the fact that four of the studies examining bird establishment came from the same location (New Zealand), and thus might be providing messages that are nonindependent. This highlights, however, one of our major points: additional, more diverse, studies are urgently needed. We concur with Rejmánek and Reichard⁵ and Gerlach⁴ about the importance of correlation among and interaction between species characteristics in determining a predisposition for becoming an invading species; we also agree with Rejmánek and Reichard⁵ that the importance of species characteristics are context dependent (as indicated by our Box 1; Ref. 1). These factors contribute to the complexity of invasions; space limitations precluded our discussing them further.

We welcome the additional relevant information from studies that did not meet the criteria that defined our literature search: the relationship between native and invaded ranges⁴; and additional important species characteristics in birds (sexual selection and behavior)³ and plants (flowering period)⁵. With regard to the latter point, the importance of length of flowering period could only be gleaned from Reichard's PhD thesis (University of Washington, 1994), which did not meet the criteria for our literature search.

Several of the respondents' points result from misunderstanding of our entries in Table 3. We are sympathetic to these misunderstandings: an editorial decision removed notation from an earlier draft that made it possible to link each entry in the table with a reference. First, Rejmánek and Reichard⁵ quote Goodwin *et al.*⁷ regarding invasiveness and flowering period. However, we classified this study as examining the Establish/Fail transition, not the Invasive/Not transition. In Goodwin *et al.*⁷, European species successfully established in New Brunswick, Canada were paired with European congeners that had not established – thus examining establishment as we defined it. Second, Sol³ discusses bird invasiveness and migratory status. Actually, we reviewed only one study examining invasiveness; three studies addressed establishment (as defined by us). The three nonsignificant entries in our table regarding establishment and migration are, indeed, from Sorci *et al.*⁸ as Sol³ seems to question. Third, the two nonsignificant entries in Table 3 regarding plant invasiveness and length of juvenile period are from Reichard and Hamilton⁹, which discusses only characteristics that significantly contributed to the multivariate models; because length of juvenile period is not mentioned, we assumed it was nonsignificant.

Finally, there are some points on which we disagree with the respondents. We disagree with Sol³ that the significant variables in the maximal model of Veltman¹⁰ and the model without phylogenetically independent contrasts of Green¹¹ are irrelevant. Similarly, we disagree with Sol's assertion³ that Sorci *et al.*⁸ did not test whether bird body mass contributed to establishment. It was not significant in an earlier model, and was hence dropped from the final model in Sorci *et al.*⁸ We also disagree with Gerlach's reading⁴ of Lonsdale¹². Upon rereading Lonsdale¹², we are satisfied that our equating Lonsdale's

'weedy' with our 'invasive' is reasonable. Most of the definitions provided by Lonsdale for 'weedy' are consistent with widespread uses by ecologists of 'invasive'. Gerlach seems to question the validity of Lonsdale's findings that origin was not significantly related to invasiveness, and that taxon and seed weight were related to invasiveness. Perhaps interaction between characteristics in these instances is important; Lonsdale did not examine them, however. We did not judge the statistical methods in studies reviewed; rather for the studies that met our criteria, we took results at face value.

Overall, then, respondents have augmented our review with useful additional information, caveats, and corrections that we are pleased to acknowledge. Many of the respondents' contributions provide further support for (and none undermine) our major point: quantitative analysis of characteristics of species is a tool that promises to be useful in studies examining community assembly and in risk assessments and management of invading species.

Cynthia S. Kolar*

David M. Lodge

Dept of Biological Sciences, Box 369,
University of Notre Dame, Notre Dame,
IN 46556, USA.

*e-mail: kolar.2@nd.edu

References

- 1 Kolar, C.S. and Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204
- 2 Enserink, M. (1999) Biological invaders sweep in. *Science* 285, 1834–1836
- 3 Sol, D. (2001) Predicting invaders. *Trends Ecol. Evol.* 16, 544
- 4 Gerlach, J.D., Jr (2001) Predicting invaders. *Trends Ecol. Evol.* 16, 545
- 5 Rejmánek, M. and Reichard, S. (2001) Predicting invaders. *Trends Ecol. Evol.* 16, 545–546
- 6 O'Connor, R.J. (1986) Biological characteristics of invaders among bird species in Britain. *Philos. Trans. R. Soc. London Ser. B* 314, 583–598
- 7 Goodwin, B.J. *et al.* (1999) Predicting invasiveness of plant species based on biological information. *Conserv. Biol.* 13, 422–426
- 8 Sorci, G. *et al.* (1998) Plumage dichromatism of birds predicts introduction success in New Zealand. *J. Anim. Ecol.* 67, 263–269
- 9 Reichard, S.H. and Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* 11, 193–203
- 10 Veltman, C.J. *et al.* (1996) Correlates of introduction success in exotic New Zealand birds. *Am. Nat.* 147, 542–557
- 11 Green, R.E. (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol.* 66, 25–35
- 12 Lonsdale, W.M. (1994) Inviting trouble: Introduced pasture species in northern Australia. *Aust. J. Ecol.* 19, 345–354