

Assessing species invasions as a cause of extinction

Anthony Ricciardi

Redpath Museum, McGill University, Montreal, QC H3A 2K6, Canada

In a recent Opinion in *TREE* [1], Gurevitch and Padilla question the generalization that biological invasions are a leading cause of species extinctions. The authors note that declines of native species frequently overlap in space and time with invasions by alien species, and these co-occurrences are sometimes used to infer a causal relationship – a potentially erroneous conclusion given that a common factor, such as physical habitat alteration, might promote both extinction and invasion. The authors further point out that extinctions are often attributable to multiple causes without any indication of the relative importance of invasions, which might be ‘merely correlated with other problems’. But I believe they chose a poor example to highlight this point.

Citing the case of native unionid mussels in North America, Gurevitch and Padilla assert that the role of zebra mussels *Dreissena polymorpha* in their decline is unclear because unionid declines began long before zebra mussels were introduced. It is indisputable that most North American unionid species have been declining for over a century owing to various anthropogenic stressors. However, empirical modeling [2] suggests that dense zebra mussel colonization has accelerated the local extinction of unionid species by a factor of 10. For example, after having survived decades of environmental degradation in the St Lawrence River, several unionid populations declined precipitously and were wiped out within a few years after invasion by zebra mussels [3]. Unionid population mortality across a range of sites in the Great Lakes–St Lawrence River basin is strongly correlated to the intensity of zebra mussel fouling on unionid shells [4]. Such fouling has been shown to interfere with normal unionid metabolism [5], and unionid survivorship increases after experimental removal of attached zebra mussels [6]. Furthermore, mark–recapture studies reveal that unionid populations can maintain high annual survival rates at sites where zebra mussels are scarce or absent, but decline rapidly with increasing zebra mussel densities across sites in the same habitat [7]. Thus, although no global extinction has yet been attributed to zebra mussel invasion, there are several lines of evidence demonstrating the role of zebra mussels as a major cause of unionid population extinctions.

The example above raises another issue. Although I agree with Gurevitch and Padilla that a critical synthesis of data is needed to assess the relative importance of invasions as a cause of extinction, I would add that such a synthesis should focus on extinction at the population level. Examining population extinctions would enable us to quantify the effect of invasions on the rate at which a species is proceeding towards global extinction [2] and would also result in a more complete understanding of their impact on biodiversity loss. A species might undergo a significant range contraction, losing many distinct populations in the process, without becoming a global extinction statistic. Given that a species typically has hundreds of genetically distinct populations [8], any analysis that tallies only global extinctions will overlook a substantial portion of biodiversity loss caused, in whole or in part, by species invasions.

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Corresponding author: Anthony Ricciardi (tony.ricciardi@mcgill.ca).

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