

Invasion biology and conservation biology: time to join forces to explore the links between species traits and extinction risk and invasiveness

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Expansion and decline of species are natural phenomena (Levin, 2000). However, owing to the increasing influence of humans worldwide, the processes driving expansion and decline have speeded up dramatically. Hence, we have the current biodiversity crisis. Human-mediated forces are making some species rarer (ie, driving them towards extinction) while at the same time making some species expand their ranges ('invasive' *sensu* Richardson *et al.*, 2000). Undisputedly, the immediate causes for extinction of native species and invasiveness of aliens are extrinsic factors, such as habitat destruction and climate change. However, the ultimate causes have to be ecological and life-history characteristics of species (Kotiaho *et al.*, 2005). Therefore, important research directions in conservation biology and invasion biology are the analyses of species traits associated with rarity (Murray *et al.*, 2002)

and invasiveness (Pyšek and Richardson, 2007), respectively. The first are important for prioritizing conservation efforts, and the second are important for prioritizing eradication efforts and the development of screening protocols of potential invasiveness of species considered for introduction to other regions.

Unravelling the links between species traits and extrinsic factors is highly complex, particularly because assessment of the causes of rarity and invasiveness relies mainly on retrospective analyses since large-scale controlled experiments are often not feasible (Richardson *et al.*, 2004). However, with the increasing availability of large, widely accessible databases and analytical approaches (eg, Wilson *et al.*, 2007), it is becoming easier to test which traits are associated with rarity and invasiveness, and under which conditions.

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To date, conservation biologists and invasion biologists have searched separately for species traits associated with rarity and invasiveness, respectively. This is surprising because the same data sets offer insights for both issues. Moreover, conservation biologists and invasion biologists encounter similar problems in their search for determinants of rarity and invasiveness, and could benefit from each other's solutions. Furthermore, one would intuitively expect rarity and invasiveness to be on opposing ends of the species trait spectrum. For example, while excessive long-distance dispersal, caused by increased fecundity in the absence of key natural enemies, is frequently a crucial factor facilitating invasion of alien species, insufficient long-distance dispersal, due to disruption of reproduction, might threaten native species (Trakhtenbrot *et al.*, 2005). If this 'opposite-ends-of-the-spectrum' hypothesis holds for most traits, information on species attributes of rare species could be used to predict attributes of potential invaders and *vice versa*, when accurate data on one of these groups is lacking. Therefore, a closer collaboration between the two groups of researchers by sharing databases and methodology could benefit both research disciplines.

Reviews of studies comparing traits of rare and common plant species conclude that there is some, albeit limited, evidence for consistent predictors of plant rarity (Bevill and Louda, 1999; Murray *et al.*, 2002). Similarly, a recent review of studies comparing invasive with either native or unsuccessful alien plant species concludes that there is some, albeit limited, evidence for consistent predictors of plant invasiveness (Pyšek and Richardson, 2007). One pattern that appears is the generally high fecundity of invasive alien species (Pyšek and Richardson, 2007) and the generally low fecundity of rare species (Murray *et al.*, 2002). Furthermore, Pandit (2006) found that, among 1183 species in the Indian subcontinent, endangered species have fewer chromosomes than non-endangered ones,

while invasive species have more chromosomes than non-invasive ones. For many other traits, however, the patterns are not clear for several reasons. Insufficient data exist for many traits, particularly those that need to be assessed experimentally (van Kleunen and Johnson, 2007). For example, only a few studies have explored how interspecific variation in phenotypic plasticity of traits is related to rarity (Murray *et al.*, 2002) or invasiveness (Richards *et al.*, 2006). In addition, it is difficult to compare studies directly because they apply different criteria in defining rarity and invasiveness, they often use small sample sizes, and they assess rarity or invasiveness at different spatial scales. Moreover, for studies on invasiveness, the control group differs between studies; some used native species and others used non-invasive alien species as control (Pyšek and Richardson, 2007). Although the latter approach is preferable (Hamilton *et al.*, 2005; Muth and Pigliucci, 2006), some of these studies have not considered whether the non-invasive alien species have actually been introduced (but see van Kleunen *et al.*, 2007).

An important distinction that most studies comparing rare and common native species do not make is the one between species that have been rare for a very long time (eg, many endemic species) and those that have become rare recently. This distinction is critical because species of the first group might have (evolved) traits that allow them to persist in small populations and prevent them from going extinct (Rabinowitz, 1981; Gaston, 1994; Gaston and Kunin, 1997). Species of the other group may have become rare recently owing to human-mediated habitat changes – to some extent because they lack such traits. Interestingly, this could explain why some species that are rare in their native range (and have been so prior to human-mediated disturbance) can spread rapidly from small founder populations when introduced to new areas. Clearly, the evolutionary history of some species has equipped them for conquests as aliens. For example, many pine

species that spread rapidly from small refugia after historical periods of glaciation are now invasive in other parts of the world (Richardson and Rejmánek, 2004). When one does not distinguish between species that have been rare for a long time and the ones that have become rare recently, it might be impossible to find attributes associated with species rarity.

Although apparent discrepancies among studies may be artifacts of different definitions of invasiveness and rarity and the lack of control for the role of extrinsic factors, it may also indicate that predictors of rarity and invasiveness are highly context-specific (Alpert *et al.*, 2000). Therefore, when framed in an objective, biogeographical context, one might expect life-history traits to be more strongly associated with invasiveness (but see Hamilton *et al.*, 2005) and rarity. Moreover, when considered in the same biogeographical context, one might find endangered native and invasive alien plants to be at opposite ends of the species traits spectrum.

Insufficient information is available to enable us to conclude that rarity and invasiveness of plants can be predicted from species attributes and that they involve the same set of traits. If the latter is true, both conservation biologists and invasion biologists would profit because data on traits of threatened rare species could be used to predict the fate of species introduced to new areas and *vice versa*. A better understanding of the correlates of human-induced rarity in native species might also benefit control programmes against invasive alien species whose aim is usually to make the species rare or, ideally, (locally) extinct (Panetta, 2007). Therefore, we suggest that conservation and invasion biologists should combine forces to improve our understanding of the links between species attributes and rarity and invasiveness. Collaboration by sharing databases and methodology will benefit both research fields.

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