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Do invasive species have bigger seeds? Evidence from intra- and inter-specific comparisons

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Abstract

Shifts in seed mass associated with the process of plant invasion may potentially enhance the competitiveness of introduced species and contribute to invasiveness. Here we test this premise using two complementary approaches. Firstly we compare the seed mass of 114 species from 31 families in both their native and introduced ranges. Secondly we compare the seed mass of 376 co-occurring native and invasive species from two families (Asteraceae and Poaceae) from California. Our results demonstrate that across the 31 families there is a significant tendency for seed mass to increase from the native to invasive ranges. In addition, the analysis on the two families revealed that such a shift in seed mass may contribute to invasive species having, on average, a higher seed mass than co-occurring native species in the same family. Consequently, these results suggest that invasion-associated upward shifts in seed mass may foster plant invasions by increasing the competitiveness of invasive species relative to natives.

Keywords: Asteraceae; California; Invasive species; Poaceae; Seed mass

1. Introduction

Invasive species are considered to be among the five most serious threats to natural systems and biodiversity (Wilcove et al., 1998), with the economic cost of invasive species running into $137 billion per year in the USA alone (Pimental et al., 2000). Consequently an ability to predict the invasive potential of new introductions could reduce the level of threat to natural areas (Reichard and Hamilton, 1997). However, it is unclear what aspects of the population biology of invasive species account for their "invasive" ability. Thus, predictions of the invasive potential of species are difficult.

Invasive species represent a small component of the world's flowering plants. For example, two recent compilations of invasive species list c. 550 species (Weber, 2003; Haysom and Murphy, 2003) compared to c. 250 k species of plant worldwide. Williamson and Fitter (1996) have proposed the "Tens Rule" based on analysing the incidence of invasive species in the United Kingdom. They found that on average, one in ten introduced species will escape cultivation, one in ten of these will become naturalised and form self-sustaining populations, and one in ten of these will become invasive. Since so few species that have the opportunity to, actually become invasive, it seems parsimonious to suggest that a limited number of key traits could influence this response.

A number of potential contributing factors for successful plant introductions/invasions have been suggested. These include greater disturbance which increases community susceptibility to invasion (Baker, 1974), high propagule pressure of invasive species (Lockwood et al., 2005) and the enemy release hypothesis (Mitchell and Power, 2003). These factors are likely to facilitate invasiveness by both increasing the opportunity for invasions and by increasing the competitiveness of invasive relative to native species. However, the plant traits that contribute to invasiveness are still unclear (Shea and Chesson, 2002).

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Seed germination and seedling establishment are high risk phases in the life-cycles of most plants (Harper, 1977). Consequently any differences in the way species respond to the environment may be most apparent at these stages. Thus, in the same way that differences in reproductive traits (regeneration niche *sensu* Grubb, 1977) may contribute to species coexistence (Daws et al., 2002), they may also potentially contribute to differential success between invasive and native species, i.e. preferential existence.

Reproductive success appears to be one of the few unifying features of invasiveness in earlier studies on plants. Many aspects of reproductive biology may contribute to invasiveness, including effective seed dispersal (McIntyre et al., 2005), the production of a persistent soil seed bank (Van Clef and Stiles, 2001) and seed mass (Rejmánek and Richardson, 1996; Buckley et al., 2003), although dispersal and persistence are themselves related to seed mass (Leishman et al., 2000). Amongst reproductive traits, seed mass is also likely to be pivotal because it influences two key components of plant life-history. Firstly, the seed mass of a plant is negatively correlated with the number of seeds that it produces (Leishman et al., 2000). Secondly, seed mass is positively associated with seedling survival; larger seeds generally result in larger seedlings which often have a higher probability of survival (Daws et al., 2005). For larger seeded species a higher seedling survival probability results from a greater ability to withstand either low levels of resources or various hazards (Leishman et al., 2000).

Seed mass has already been included in analyses comparing invasive and non-invasive *Pinus* species (Rejmánek and Richardson, 1996) and in determining whether there are functional types, or syndromes associated with invasiveness (Lloret et al., 2005; McIntyre et al., 2005). These studies found that for *Pinus* species, small seeded species were more likely to be invasive (Rejmánek and Richardson, 1996), while both Lloret et al. (2005) and McIntyre et al. (2005) identified functional groups of invasive species of which “large” seeded forbs were a key group. These studies suggest that seed mass is important for ‘invasiveness’. However, to better understand the traits that contribute to invasiveness, two types of studies on plant traits are needed: 1) intra-specific comparisons of individual species in their native and invasive ranges, and 2) inter-specific comparisons of co-occurring invasive and non-invasive species (Hierro et al., 2005).

Taking this general approach, Buckley et al. (2003) found that for *Cytisus scoparius*, but not for *Ulex europaeus*, that seed mass is greater in the invasive than native range. Similarly, Schmitt and Rivière (2002) found that on La Réunion the invasive species *Syzygium jambos* had larger seeds than the native con-gener *Syzygium cymosum* and Baker (1972) found, in a comparison of native and invasive forbs in California, that the invasive species had larger seeds. However, we more rigorously apply these approaches to a broad range of species. Firstly, for 114 invasive species from both Weber (2003) and Haysom and Murphy (2003), we compare seed mass values in both their native and invasive ranges. Secondly, for two key invasive families (Asteraceae and Poaceae), which together contribute c. 23% of the most serious invasive plants in Weber (2003), we compare seed mass data for co-occurring native and invasive species in California to test whether within the same family invasive species have a larger seed mass than co-occurring species. Unlike the earlier study by Baker (1972), this intra-familial as opposed to cross-species approach has the advantage that both native and invasive species in the analysis are likely to have both similar growth forms and reproductive biology, reducing the potentially confounding influence of phylogenetic un-relatedness on seed mass.

2. Materials and methods

2.1. Intra-specific comparisons

Weber (2003) and Haysom and Murphy (2003) were used to compile a list of invasive species. Weber (2003) lists native and invasive ranges for the species it contains, while Haysom and Murphy (2003) only provides species’ invasive ranges. Consequently, the Pacific Island Ecosystems at Risk, Risk Assessment (http://www.hear.org/pier), the Global Compendium of Weeds Database (http://www.hear.org/gcw) and the GRIN taxonomy database (http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl) were used to identify species’ native ranges.

For species for which both the native and invasive ranges could be identified, seed mass data was obtained from the Royal Botanic Garden Kew’s Seed Information Database (SID; Flynn et al., 2004, http://www.rbgkew.org.uk/data/sid). For the seed mass data, the original source references were checked to determine whether seed collections came from the native or invasive range and to verify the seed mass data. This approach resulted in 114 species for which we had seed mass data for both ranges (see Appendix A for families and genera included in this analysis). For different species, seed mass data in SID is presented on a fresh, air-dried or oven-dried basis with it often being unclear (from the scientific literature) how seed mass has been determined. In addition, the unit for which seed mass is reported can vary between studies (seed, fruit, dispersule, propagule etc.). Consequently, we assumed that such variations in the means of reporting seed mass were random across our dataset, i.e. there was no systematic bias in the method of determination/reporting seed mass in relation to native and invasive ranges.

2.2. Inter-specific comparisons

The Baker seed mass dataset (Baker, 1972), contains seed mass data for c. 2500 taxa that occur in California, including a wide range of invasive species. Subsequently, for the two largest families containing invasive species in the dataset (Asteraceae and Poaceae), all seed mass values were extracted from the Baker dataset and, as in the analysis by Baker (1972), species assigned as either ‘native’ or ‘invasive’ based on Munz (1959). Species were classified as invasive when they were referred to as both ‘non-native’ and