



Contents lists available at SciVerse ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Mutualism vs. antagonism in introduced and native ranges: Can seed dispersal and predation determine *Acacia* invasion success?

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ARTICLE INFO

Article history:

Received 9 October 2012

Received in revised form 25 February 2013

Accepted 2 March 2013

Available online 6 April 2013

Keywords:

Biological invasion

Density-dependence

Establishment

Exotic

Plant–animal interactions

Weed

ABSTRACT

Plant species introduced to new regions can escape their natural enemies but may also lose important mutualists. While mutualistic interactions are often considered too diffuse to limit plant invasion, few studies have quantified the strength of interactions in both the native and introduced ranges, and assessed whether any differences are linked to invasion outcomes. For three *Acacia* species adapted for ant dispersal (myrmecochory), we quantified seed removal probabilities associated with dispersal and predation in both the native (Australian) and introduced (New Zealand) ranges, predicting lower removal attributable to dispersal in New Zealand due to a relatively depauperate ant fauna. We used the role of the elaiosome to infer myrmecochory, and included treatments to measure vertebrate seed removal, since this may become an important determinant of seed fate in the face of reduced dispersal. We then tested whether differences in seed removal patterns could explain differences in the invasion success of the three *Acacia* species in New Zealand.

Overall seed removal by invertebrates was lower in New Zealand relative to Australia, but the difference in removal between seeds with an elaiosome compared to those without was similar in both countries. This implies that the probability of a removed seed being dispersed by invertebrates was comparable in New Zealand to Australia. The probability of seed removal by vertebrates was similar and low in both countries. Differences in the invasive success of the three *Acacia* species in New Zealand were not explained by differences in levels of seed predation or the strength of myrmecochorous interactions. These findings suggest that interactions with ground foraging seed predators and dispersers are unlikely to limit the ability of *Acacia* species to spread in New Zealand, and could not explain their variable invasion success.

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Introduction

A leading hypothesis for the success of alien plant species introduced to new regions is that they benefit from leaving behind natural enemies, such as seed predators, that regulate the population in the native range (Keane and Crawley, 2002). However, introduced plant species may also leave behind mutualists, such as seed dispersers, which are important in population spread. Although mutualistic interactions are often considered diffuse, in that many organisms can provide similar functions such that alien plants are likely to encounter suitable mutualists in novel environments (Horvitz and Beattie, 1980; Traveset and Richardson, 2006; Montesinos et al., 2012), there is evidence that the loss of some mutualists can have negative impacts on alien plant performance

that outweigh any advantages of enemy release (Morris et al., 2007; Pringle et al., 2009; Dickie et al., 2010). In addition, most studies that examine the role of mutualists in alien plant invasion focus on well-established and often problematic alien plants that are likely to have formed successful mutualisms (e.g. Glyphis et al., 1981; Rodríguez-Echeverría et al., 2009; Montesinos et al., 2012). Consequently, the role that loss of mutualists might play in the failure of alien species to establish and spread may have been underestimated.

Seed dispersal is a key process in the establishment and spread of plant populations (Forget et al., 2005) and for most alien species sufficient seed must escape seed predators and be dispersed away from parent plants for successful invasion. While escaping natural enemies and forming new dispersal mutualisms may contribute to the success of some invasive species (Buckley et al., 2006; Dawson et al., 2009), it is unclear whether failing to do so is the reason why many other species fail to establish and spread. Understanding this requires quantifying biotic interactions in both the native

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and introduced ranges of alien plant species that differ in their invasive ability, comparisons that are rarely undertaken (Hierro et al., 2005). Here, we fill this gap by quantifying the importance of putative seed dispersers and seed predators in both the native and introduced ranges of three congeneric alien plant species that differ in the degree to which they have established and spread. We studied Australian species in the genus *Acacia* that have been introduced to New Zealand, where escape from a key dispersal mutualist could be critical in both preventing effective seed dispersal and increasing rates of seed predation.

Australian *Acacia* species have been introduced widely around the world, primarily for forestry and horticulture. While several species are invasive throughout their introduced range (Richardson and Rejmánek, 2011), many have failed to establish or spread following introduction Richardson et al. (2011). Most Australian *Acacia* species have seeds adapted for dispersal by either birds (ornithochorous species) or ants (myrmecochorous species) (O'Dowd and Gill, 1986). Myrmecochorous species possess a lipid-rich appendage (elaiosome) that acts as a food reward and a handle to assist seed movement by ants (Mayer et al., 2005). Myrmecochory is thought to benefit seed dispersal through protecting seeds from predation and fire, by removing them underground, reducing intraspecific competition, by redistributing seeds away from parent trees, and increasing the rate of seed movement to more favourable microhabitats (Giladi, 2006).

Myrmecochorous *Acacia* seeds fall to the ground soon after pod dehiscence. Once on the ground they are usually removed by ants, although birds, small mammals and other invertebrates may also remove seeds (Hughes and Westoby, 1990). Predation of seeds by granivorous ants can account for almost all seed removal, depending on the species involved (Ireland and Andrew, 1995). However, seed removal by ants can result in dispersal (myrmecochory) when ants transport seeds to their nest, usually only a few metres from parent trees (Ness et al., 2004), but then discard the seed. Seeds are often discarded underground, where the hard coat of *Acacia* seeds allows them to persist in the seed bank for several decades (Auld, 1986). Where present, ants and other invertebrates may also eat the elaiosome *in situ* (Berg, 1975; Auld, 1986; Beaumont et al., 2011), reducing the likelihood of subsequent ant dispersal (Auld, 1986; Ireland and Andrew, 1995) and thus further leaving seeds exposed to predation (Hughes and Westoby, 1990; Auld and Denham, 1999).

At least 150 species of Australian *Acacia* have been introduced to New Zealand (Diez et al., 2009), of which 17 have naturalised, defined as having established self-sustaining populations (Howell and Sawyer, 2006), and eight are sufficiently widespread to be classed as environmental weeds (Howell, 2008). All but two of the species that have naturalised in New Zealand are myrmecochorous. The variable success of myrmecochorous *Acacia* species in establishing and spreading may be due to differences among species in their ability to form dispersal mutualisms, particularly as, relative to Australia, New Zealand has a depauperate ant fauna with lower ant densities (Ward, 2009). While there are more than 15,000 ant species in Australia (CSIRO, 2012), and approximately 1500 myrmecochorous plant species (Berg, 1975), New Zealand has only 11 native and 29 introduced ant species (Don, 2007; Landcare Research, 2012) and no confirmed native myrmecochorous plants (Thorsen et al., 2009). If seed dispersal by ants is important in *Acacia* population dynamics then these species may be at a disadvantage in New Zealand due to reduced seed dispersal, even if they concurrently escape ant granivory. Lower rates of removal by ants may also leave seeds exposed to vertebrate predators as introduced granivorous rodents are widespread in New Zealand (Williams et al., 2000).

Since a function of the elaiosome is to elicit seed removal by ants (Berg, 1975; Auld, 1986), the increase in the removal rate of

seeds with an elaiosome, relative to those without, is frequently used to infer the importance of myrmecochory in seed fate (Hughes and Westoby, 1990; Pemberton and Irving, 1990). However, an increase in seed removal associated with elaiosome presence might not translate directly to dispersal if granivorous ants preferentially remove and consume those seeds (Hughes and Westoby, 1990, 1992a; Ireland and Andrew, 1995). Determining the ultimate fate of seeds is difficult without following individual seeds, or excavating ant nests to estimate the proportion of seeds removed by ants that have been eaten rather than discarded intact (e.g. Auld, 1986; Hughes and Westoby, 1992b; Ireland and Andrew, 1995). Nevertheless, when these studies have been undertaken, the results suggest that elaiosome presence does increase the probability of seed removal by ant species that disperse seeds (Auld, 1986; Ireland and Andrew, 1995). In addition, these ants show a stronger preference for seeds with an elaiosome, relative to seeds without, than species that act mainly as seed predators (Hughes and Westoby, 1992a; Hughes et al., 1994). Differences in the probability of removal for seeds with and without an elaiosome can therefore measure the strength of myrmecochory and thus the relative potential for seed dispersal.

We carried out diaspore removal experiments, where diaspore refers to the unit of dispersal (either the seed alone or the seed plus elaiosome), to quantify the probability of seed removal for three species of myrmecochorous *Acacia* that differ in the degree to which they have established and spread following introduction to New Zealand. We examined the probability of seed removal by invertebrates and used the presence or absence of an elaiosome to infer the strength of myrmecochory, and hence the relative potential for dispersal by ants, in both the native (Australia) and introduced (New Zealand) ranges. We also quantified the probability of removal by vertebrates, to identify whether vertebrate seed predation is more important where dispersal by ants is reduced.

We used this study system to answer three questions:

1. Does the probability of diaspore removal by invertebrates differ between New Zealand and Australia? We expect both higher overall removal probabilities and a stronger influence of the elaiosome on removal probability in Australia, relative to New Zealand, due to the more diverse and abundant ant fauna.
2. Does the probability of vertebrate removal differ between countries? In Australia seed removal by vertebrates is low, relative to invertebrates (e.g. Hughes and Westoby, 1990), but this could differ in New Zealand if ant removal is reduced and because there is a different suite of vertebrate predators.
3. Can differences in the probability of seed removal by invertebrates and/or vertebrates explain the differential invasion success of *Acacia* species introduced to New Zealand? If seed dispersal and/or seed predation are important determinants of species' invasion success we predict that more invasive *Acacia* species would have a higher probability of removal attributable to myrmecochory and/or lower seed predation probabilities.

Methods

Study species

From the pool of *Acacia* species that have been introduced to New Zealand we selected three myrmecochorous species that differed in the degree to which they have naturalised and spread (Table 1). All species are native to south-eastern Australia, a region with a close climate match to New Zealand (Kriticos, 2012). *Acacia dealbata* Link is widespread and common throughout south-eastern Australia (Maslin, 2001) and is invasive in New Zealand,

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