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Original article

Site-specific conditions influence plant naturalization: The case of alien Proteaceae in South Africa

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ABSTRACT

The outcome of plant introductions is often considered in binary terms (invasive or non-invasive). However, most species experience a time lag before naturalization occurs, and many species become naturalized at some sites but not at others. It is therefore important to understand the site-specific mechanisms underlying naturalization. Proteaceae is an interesting case as some species are widespread invaders, while others, despite a long history of cultivation, show no signs of naturalization. At least 26 non-native Proteaceae species have been introduced to, and are cultivated in, South Africa. We mapped populations and examined differences between naturalized and non-naturalized populations (e.g. propagule pressure, land use and bioclimatic suitability). Of the 15 species surveyed, 6 were naturalized at one or more sites. Of these, *Hakea salicifolia* is most widely cultivated, but is only naturalizing in some areas (32 naturalized populations out of 62 populations that were surveyed). We found propagule pressure to be the most important determinant of naturalization for *H. salicifolia*. However, in suboptimal climatic conditions, naturalization only occurred if micro-site conditions were suitable, i.e. there was some disturbance and water available. For the other naturalized species there were few sites to compare, but we came to similar conclusions – *Banksia integrifolia* only naturalized at the site where it was planted the longest; *Banksia serrata* only naturalized at a site influenced by fire regimes; while *Banksia formosa* naturalized at sites with high propagule pressure, absence of fires and where there is no active clearing of the plants. Naturalization of Proteaceae in South Africa appears to be strongly mediated by site-specific anthropogenic activities (e.g. many planted individuals and water availability). More broadly, we argue that invasion biology needs to focus more closely on the mechanisms by which species and pathways interact to determine the likelihood and consequence of an invasion.

1. Introduction

Only a subset of introduced species become naturalized and only a subset of naturalized species become invasive (Williamson and Brown, 1986). Different factors assume particular importance at different spatial scales and at different stages of the introduction-naturalization-invasion (INI) continuum (Blackburn et al., 2011; Richardson and Pyšek, 2012), but in general naturalization and invasion is the result of an interaction between species traits, features of a site, and introduction dynamics. Each of these three factors has been studied in depth. For example, Pyšek and Richardson (2007) reviewed the influence of species traits; various features of a site have been studied [e.g. climate (Richardson and Thuiller, 2007), land use and human-mediated disturbance (Vilà and Ibáñez, 2011)]; while introduction dynamics such as propagule pressure (Colautti et al., 2006; Lockwood et al., 2005), and residence time (Wilson et al., 2007) have been the focus of many studies. However, fewer studies have explored the interactions between species traits, introduction dynamics, and features of a site.

Climatic suitability (an interaction between species traits and the prevailing climatic conditions at a site) is generally considered a prerequisite for naturalization and invasion (Guisan and Thuiller, 2005; Mack, 1996). However, introduction dynamics such as high propagule pressure can sometimes overcome barriers imposed by

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suboptimal environmental conditions (Rejmánek et al., 2005b). Species introduced in large numbers over a long period of time have a greater chance of establishing and spreading than those with lower propagule pressure (Dehnen-Schmutz and Touza, 2008; Lockwood et al., 2005; Rouget and Richardson, 2003; Simberloff, 2009). In addition, plants occupying an area for a longer period have a greater chance to disperse more propagules, experience more favourable recruitment events and have a longer time for suitable phenotypes to be selected that can cope with local conditions (Pyšek et al., 2009; Rejmánek et al., 2005a).

One way to test these ideas is to examine the outcome of introducing several species to several localities in different ways (what has been termed a large unplanned natural experiment in invasion science). Along this line work on several model groups in plant invasion ecology, such as Australian acacias and *Pinus* species, has provided general predictors (Rejmánek and Richardson, 1996; Richardson et al., 2011). Here we use Proteaceae as a test case.

Proteaceae is a large family of flowering plants with a long history of introduction to many parts of the world, mainly for horticulture (Sedgley et al., 2007). Although evidence from around the world suggests that Proteaceae is not a particularly "weedy" family (only 8 species of the 402 introduced species are recorded as invasive; Moodley et al., 2013), this may be due at least partly to the fairly recent history of introductions for many species. These recently introduced species are not yet invasive but might form part of the "invasion debt" (Essl et al., 2011). Given that many species have been introduced to many localities and these species occupy different stages in the invasion continuum, Proteaceae provides an excellent group to identify possible site-specific factors that are likely to drive biological invasions. Because of the growing commercial interest, there is also a need for post-border risk assessments in this group (Wilson et al., 2013).

South Africa in particular has a substantial number of alien Proteaceae (hereinafter referred to as proteas), which were introduced for use as barrier plants, ornamental purposes, food, cut-flowers and as landscape plants. At least 26 proteas have been introduced into South Africa (SAPIA, accessed November 2011; Rebelo, 1991–2001; pers. obs.) of which 11 species are recorded as naturalized (Fig. 1). Three of these species (*Hakea drupacea* (C.F.Gaertn.) Roem. & Schult., *Hakea gibbosa* (Sm.) Cav., and *Hakea sericea* Schrad. & J.C.Wendl.) have become widespread invaders in South Africa, although in each case there are still climatically suitable areas of the country that are not yet invaded (Le Maitre et al., 2008; Richardson et al., 1987; Rouget et al., 2004).

For other naturalized proteas we are beginning to understand the drivers of invasion, which include the presence of a suitable fire regime (Geerts et al., 2013). In addition, many species are extensively cultivated (i.e. high introduction efforts) but have not yet become naturalized. For example, South Africa is one of the largest producers of macadamia nuts in the world and has for many years been home to large plantations of *Macadamia integrifolia* Maiden & Betche, *M. tetraphylla* L.A.S. Johnson and cultivars of these species (Mabiletsa, 2004; Nagao, 2011; The Southern African Macadamia Growers' Association, http://www.samac.org.za), but there are no records of the genus naturalizing in southern Africa (SAPIA, accessed May 2013). The seeds of these species are dispersed by water (Department of Sustainability, Environment, Water, Population and Communities (2013), http://www.environment.gov.au/sprat). Therefore the location of these plantings (gardens and orchards) may be preventing its spread. This suggests that there is potential for future naturalization since these species may be in a lag phase. Finally, evidence is emerging that some introduced Proteaceae species with a long history in South Africa are starting to become naturalized, but only at a few sites. For example, anecdotal observations suggest that *Hakea salicifolia* (Vent.) B.L. Burtt, a species widely planted as a hedge plant for at least a century, is starting to spread.

Of the naturalized Proteaceae in South Africa, *H. salicifolia* is intermediate in its adventive distribution. The species was for many years considered non-invasive. It was not listed among 84 "emerging invaders" in a national study that aimed to prioritize alien plant species and areas for management action (Nel et al., 2004). Although not listed under current legislation, it has been considered for listing, and therefore an assessment of the threats it poses is overdue (Wilson et al., 2013).

H. salicifolia has a wide planted distribution in South Africa where it is used as a hedge plant and for windbreaks across the fynbos, grassland and savanna biomes. It has naturalized and become invasive in several regions of the world (Table 1). It is an obligate seeder and possesses follicles that afford some protection for the seeds against fire (Protea Atlas Database). In New Zealand fires have successfully assisted the spread of *H. salicifolia* (Williams, 1992). However, in South Africa the lack of spread into fynbos vegetation has been attributed to thin follicle walls that are unable to protect seeds from typical fynbos fires (Richardson et al., 1987).

This study aimed to (1) determine the invasion status of introduced Proteaceae species in South Africa which are not classified as major invaders; (2) conduct a qualitative assessment of factors explaining naturalization for Proteaceae species in South Africa; and (3) quantitatively analyse factors that predict naturalization for species that have many naturalized and non-naturalized populations (*H. salicifolia* being the only example with sufficient data for detailed analysis).

2. Methods

2.1. Study sites

We compiled a list of all recorded localities of alien proteas in southern Africa, using the Protea Atlas Database and the Southern African Plant Invaders Atlas (SAPIA) as initial sources (SAPIA, accessed November 2011; The Protea Atlas Project, accessed August 2011). Following detailed field searches we also added personal observations and information provided by farmers and land owners to the locality list. Our aim was to understand which site factors are important for triggering naturalization (i.e. transition from introduction to naturalization; Richardson and Pyšek, 2012); we therefore excluded *H. drupacea*, *H. gibbosa*, and *H. sericea*. It is illegal to

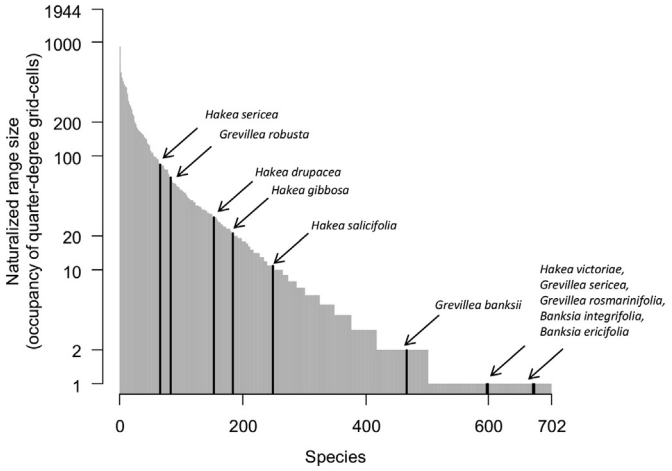

Fig. 1. Ranked bar plot showing the naturalized range sizes of alien plants in South Africa (log scale) with naturalized Proteaceae highlighted in black. The data were derived from the SAPIA database, accessed November 2011.