



Human-mediated introductions of Australian acacias – a global experiment in biogeography

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ABSTRACT

Aim Australian acacias (1012 recognized species native to Australia, which were previously grouped in *Acacia* subgenus *Phyllodineae*) have been moved extensively around the world by humans over the past 250 years. This has created the opportunity to explore how evolutionary, ecological, historical and sociological factors interact to affect the distribution, usage, invasiveness and perceptions of a globally important group of plants. This editorial provides the background for the 20 papers in this special issue of *Diversity and Distributions* that focusses on the global cross-disciplinary experiment of introduced Australian acacias.

Location Australia and global.

Methods The papers of the special issue are discussed in the context of a unified framework for biological invasions. Distributions of species were mapped across Australia, their representation in bioclimatic zones examined and the potential global distribution of the group modelled. By collating a variety of different lists, we determined which Australian acacias have reached different stages in the introduction-naturalization-invasion continuum in different parts of the world. Paradigms and key research questions relating to barriers to invasion, stages of invasion and management perceptions are sketched.

Results According to our global database of Australian acacia records, 386 species have been moved outside Australia by human agency, 71 species are naturalized or weedy, and 23 are unequivocally invasive. Climatic models suggest that about a third of the world's land surface is climatically suitable for Australian acacias. Many species are commercially important crops or are useful for other purposes and have been extensively planted, and many different human perceptions of Australian acacias exist in different parts of the world. The papers in the special issue cover all the barriers, stages and processes that define biological invasions and touch on many aspects: history and the human dimension; aspects of the species pool; species traits; biotic interactions; climate and niche; and management.

Main conclusions Australian acacias are an excellent model group for examining interactions between evolutionary, ecological and socio-economic drivers of species introductions. New insights have emerged on the biological, ecological and evolutionary correlates of naturalization and invasion, but human usage factors permeate all explanatory models. Understanding and managing introduced Australian acacias requires a fundamental and integrative appreciation of both intrinsic (e.g. species traits) and extrinsic (e.g. human usage and perceptions) aspects.

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INTRODUCTION

Humans have moved species around the world for thousands of years, but the number of species involved, the rate and magnitude of movement, and the number of pathways involved have increased massively over the past three centuries (Ricciardi, 2007; Wilson *et al.*, 2009). Non-native species are now dominant components of many ecosystems. They provide goods and services that sustain burgeoning human populations, but are also important drivers of global change and, in many cases, of ecosystem alteration (Pyšek & Richardson, 2010). The human-mediated re-shuffling of the world's biota also provides opportunities for testing ecological and evolutionary theories. The scientific study of the movement of species to areas outside their natural ranges and the fate of these species in their new ecosystems has become an important subdiscipline of biogeography and ecology (Richardson, 2011a,b).

The ways in which different sectors of human societies perceive non-native species are becoming increasingly complex and change over time (e.g. Warren, 2007, 2008; Richardson *et al.*, 2008a,b). In particular, species that are commercially important or that are valued by different sectors of society, but which are also problematic invaders in parts of their range, pose special challenges for those tasked with managing natural resources. The human dimensions of invasions are receiving increased attention, drawing interest from researchers in the humanities (e.g. ethicists, historians, philosophers, sociologists) and those studying human behaviour (e.g. movement patterns; Brockmann *et al.*, 2006; González *et al.*, 2008). The rich literature on biological invasions is, however, compartmentalized—there is too little infusion of insights across disciplines (Kueffer & Hirsch Hadorn, 2008). The set of papers in this special issue of *Diversity and Distributions* aims to bring together the work of scholars in a variety of disciplines to initiate a truly comparative, multidisciplinary conversation and to encourage genuinely trans-disciplinary work. Australian acacias provide a good study system for this purpose.

Among tree genera of the world, three taxa make up a very large part of plantings of species outside their native ranges (where they may be termed alien, exotic or non-native): *Acacia* Mill. (*sensu lato*), *Eucalyptus* L'Hér. and *Pinus* L. Of these, *Acacia* and *Pinus* are particularly well represented in global lists of invasive alien species (those that have spread from introduction sites in novel environments) (Richardson & Rejmánek, 2011). *Pinus* has been well studied, both within its natural range and in the many parts of the world where pines are grown as exotics (Richardson, 1998; Richardson *et al.*, 2007). The invasion ecology and underlying mechanisms associated with range changes of pines have also been well studied (Richardson, 2006; Richardson *et al.*, 2008a,b; Carrillo-

Gavilan & Vila, 2010; Essl *et al.*, 2010; Simberloff *et al.*, 2010; Nuñez & Medley, 2011; Procheş *et al.*, 2011). Eucalypts, on the other hand, although planted at a similar grand scale worldwide, have been much less successful as invasive species, with only a handful of major invaders (Richardson & Rejmánek, 2011). Not surprisingly, the invasion ecology of eucalypts is less well known than that of pines (Rejmánek & Richardson, 2011).

Like pines and eucalypts, many acacias (a polyphyletic group comprising more than 1350 species (Maslin *et al.*, 2003); see Appendix 1 for details on taxonomy) and especially Australian acacias have been widely planted outside their natural ranges for centuries. Different species have fared differently as non-natives, even under similar environments and with similar introduction histories. Nevertheless, landscapes in many parts of the world are now dominated by planted or self-sown stands of Australian acacias. Some species are crops of major commercial importance and many others have considerable value for a wide range of purposes (Griffin *et al.*, 2011; Kull *et al.*, 2011; van Wilgen *et al.*, 2011). Some Australian acacias are among the most widespread and damaging of all invasive plants (Lowe *et al.*, 2000; Gaertner *et al.*, 2009; Richardson & Rejmánek, 2011), others are only moderately weedy, and yet others are not known to invade, although some of the last-mentioned are recent introductions (Wilson *et al.*, 2011) and likely represent a substantial invasion debt. The human perception of Australian acacias differs markedly in different parts of the world where they are grown as exotics. Even within regions, different sectors of human society view different species very differently and within distinct cultural and historical contexts (Carruthers *et al.*, 2011; Kull *et al.*, 2011). Attempts to manage Australian acacias have taken many forms in different parts of the world (Wilson *et al.*, 2011). Management policies, legislation and best-practice guidelines in different regions are the result of the complex interplay between cultural and socio-political factors, shaped by environmental drivers and disturbance regimes (e.g. Roura-Pascual *et al.*, 2010).

The long history of widespread transfers and planting of Australian acacias in many parts of the world has created an outstanding natural experiment with considerable opportunities for garnering insights into the factors that influence, for example: (1) the ways that different introduced species have been assimilated into ecosystems, local human cultures and value systems and how this has changed over time and under different circumstances; (2) why species have shown different degrees of invasiveness in new environments; (3) why certain ecosystems are more susceptible to acacia invasions than others; (4) the function of acacias in recipient environments and their capacity to alter ecosystem functioning and services; and (5) the factors that influence the evolution of management

responses in different regions. The multiple dimensions of the natural experiment may suggest new approaches and priorities for the emerging field of invasion science (Richardson, 2011b). It also has much potential for helping to shape the dimensions of and priorities for the young field of conservation biogeography which applies biogeographical principles, theories and analyses to problems regarding biodiversity conservation (Richardson & Whittaker, 2010). Alien species pose a bewildering array of challenges (and some opportunities) for conservationists, and new frameworks and tools are needed to assimilate the multitude of perspectives for devising appropriate and sustainable management strategies.

AUSTRALIAN ACACIAS AS A MODEL SYSTEM FOR INVASION SCIENCE

Australian acacias provide a good opportunity for a multidisciplinary cross-examination of the many dimensions involved in the global expansion of an important group of plants for at least the following twelve reasons:

1. The group contains a very large number of taxa (1012 species were recognized as of October 2010), at least a third of which have been moved by humans to areas outside their natural ranges (Griffin *et al.*, 2011; Tables 1 & 2; Appendix S1) of which 23 are confirmed as invasive (*sensu* Pyšek *et al.*, 2004) (Richardson & Rejmánek, 2011) and many more are naturalized (Table 1).
2. The group has a well-resolved taxonomy and phylogeny (Miller *et al.*, 2011). This provides the opportunity to explore whether invasiveness has a phylogenetic signature. Invasive and naturalized species come from several, but not all, major clades within the genus (Miller *et al.*, 2011).
3. Australian acacias are present in most major biogeographical regions in Australia (Fig. 1). Adaptations necessary to persist across such a wide range of environmental conditions mean that different taxa are pre-adapted to survive and flourish in many different parts of the world (analogous conditions to those that exist in different parts of the Australian range of *Acacia* exist in many parts of the world; Fig. 2).
4. The native-range distributions of all taxa are well known, and point-locality data are available from the Australia's Virtual Herbarium, facilitating detailed biogeographical and macroecological analyses (Hui *et al.*, 2011) and species distribution modelling (Thompson *et al.*, 2011; Webber *et al.*, 2011).
5. Many Australian acacias show exceptionally high levels of intraspecific divergence and variation (Le Roux *et al.*, 2011). As introductions of taxa to new regions have sampled different proportions of the genetic diversity of native populations, contemporary and micro-evolutionary processes and mechanisms associated with persistence and invasiveness across multiple species can be assessed both at inter- and intraspecific levels (Le Roux *et al.*, 2011; Thompson *et al.*, 2011).
6. The extensive and various human usages have involved artificial selection for various traits, many of which – such as growth rate, robustness and environmental tolerance – could potentially influence invasion success (Griffin *et al.*, 2011).

7. Australian acacias have been widely utilized for many purposes in many parts of the extra-Australian range. Receiving environments have rich and diverse socio-cultural histories that have influenced the need for introductions of Australian acacias and influence how they are assimilated into changing cultures and value systems (Carruthers *et al.*, 2011). These paved the way for a new synthesis of the full suite of human connections with Australian acacias outside their natural ranges (Kull *et al.*, 2011).

8. Introductions and the fate of plantings of Australian acacias as exotics are generally well documented (in some cases exceptionally well; e.g. Poynton, 2009), making it feasible to explore factors associated with successes and failures and testing the validity of particular paradigms associated with different introduction histories, e.g. multiple versus single introduction events (Le Roux *et al.*, 2011), the role of different ecophysiological and life-history traits (Castro-Díez *et al.*, 2011; Gallagher *et al.*, 2011; Gibson *et al.*, 2011; Morris *et al.*, 2011) and features of natural ranges (Hui *et al.*, 2011) in determining invasiveness, and how metrics of human usage interact with these factors (Castro-Díez *et al.*, 2011).

9. A few species have been very widely planted in massive numbers in commercial plantations (Griffin *et al.*, 2011). Introduced Australian acacias are now dominant components of ecosystems in many parts of the world (Fig. 3), where contrasting conditions have exposed them to a wide range of potential habitats and novel biotas.

10. A large literature exists on many aspects of Australian acacias as non-native species, facilitating interspecific comparisons on many fronts.

11. Introductions of Australian acacias to a wide range of ecosystems provide many opportunities to explore interactions between trophic levels that contribute to invasive success (notably in the case of mutualisms involving soil microbiota; Rodríguez-Echeverría *et al.*, 2011), mediate their influence on native biota (Le Maitre *et al.*, 2011; Veldtman *et al.*, 2011) and affect the health of species of commercial importance (Wingfield *et al.*, 2011).

12. Similarly, the long history of management in some countries, but relatively recent initiation of interventions in others, creates an ideal situation for exchanging lessons and building generalizations for best practice (Le Maitre *et al.*, 2011; Moore *et al.*, 2011; van Wilgen *et al.*, 2011; Wilson *et al.*, 2011).

This paper provides background and context for the wide range of issues covered in the special issue within a proposed unified framework for biological invasions (Blackburn *et al.*, 2011) (Fig. 4). The following sections elucidate some of the key factors that have shaped (and continue to shape) the global expansion of Australian acacias. Particular attention is given to themes touched upon in the special issue papers.

THE SPECIES POOL: AUSTRALIAN ACACIAS AT HOME

Acacia subgenus *Phyllodineae* has undergone spectacular radiations in Australia. Of the 1022 species in subgenus

Table 1 Lists of Australian *Acacia* species relevant to different points on the introduction-naturalization-invasion continuum.

List	Usage	Numbers	Description	References	
Australia	All <i>Acacia</i> species in subgenus <i>Phyllodineae</i> that have Australia as part of their native range	Total number of species (also used as a reference list of names)	1012 (A–E) [note there are a total of 1022 <i>Acacia</i> species in subgenus <i>Phyllodineae</i>]	The list of valid species as defined in the special issue. Hybrids and crosses are not included, and infra-specific information is ignored. There are several groups, in particular the <i>Acacia aneura</i> complex, where new species are currently being described and it is estimated that there are up to 100 undescribed species (Maslin <i>et al.</i> , 2003). However, given the extensive taxonomic work performed on this group in Australia, it is likely this list represents 90% of species. Most of these species are native exclusively to Australia, only 17–20 species have a native range extending outside Australia and only 10 are exclusively non-Australian. There are also two species of <i>Acacia</i> subgenus <i>Aculeiferum</i> and seven species of <i>Acacia</i> subgenus <i>Acacia</i> native to Australia.	Australia's Virtual Herbarium (accessed 29 June 2010); World Wide Wattle, (accessed Dec. 2010); B. Maslin (pers. comm., 2010, 2011)
Global	All records of introduction	Number of introduced species	386 (A2–E)	The number of Australian acacias that have been introduced to countries outside Australia, a combination of all the lists below. While there are many clear examples of human-mediated dispersal of acacias within Australia, these are not included as intra-Australia dispersal cannot always be definitively ascribed to human activities.	This paper
	All records of naturalization	Number of naturalized species	71 (C2–E)	The number of Australian acacias that have naturalized in countries other than Australia according to Global Compendium of Weeds (GCW). This list includes one species, <i>A. holosericea</i> , that has been recorded as invasive but was not included in the GCW at the time the database was accessed.	This paper
	Confirmed records of invasion	Number of invasive species	23 (E)	Data on Australian acacias from a global review of invasive alien trees and shrubs. The list only includes species for which there is clear evidence of invasion (<i>sensu</i> Pyšek <i>et al.</i> , 2004).	Richardson & Rejmánek (2011)
	Australian Tree Seed Centre (ATSC)	Number of introduced species	299 (A2–E)	Export records of seed-lots sent from Australian Tree Seed Centre (CSIRO, Australia) to other countries around the world, 1980–2010. Data on the number of regions to which seed-lots were sent, and the number of seed-lots are also available (total of 49,052 seed lots).	Griffin <i>et al.</i> (2011)
	18th and 19th century introductions	Number of introduced species	98 (A2–E)	List of species introduced and cultivated in Europe. This represents among one of the first waves of botanical samples sent from Australia. Many of the species were likely sent on from their original location. Around 178 introductions can be tied to current names, but a further 40 or so are only known by their horticultural names.	Cavanagh (2006)
	Herbarium records (GBIF)	Number of introduced species	143–151 (A2–E)	This list, based on 5580 herbarium records, is of samples collected outside Australia. The list is taken as evidence that mature plants were grown outside Australia at some point in time. As 8 species recorded have native ranges extending outside Australia, there is some uncertainty about whether the herbarium records collected for these plants were following an introduction. Around 5% of all herbarium records downloaded were not used as they could not be given a valid name, or rejected as an obvious error, or removed because of no location data.	Global Biodiversity Information Facility (accessed 20 July 2010)

Table 1 Continued.

List	Usage	Numbers	Description	References	
Global Compendium of Weeds (GCW)	Number of naturalized and number of invasive species	70 (C3–E) 16 (E)	Based on records returned from a search of the term ‘ <i>Acacia</i> ’ in the GCW. After sorting for valid Australian acacias and excluding 7 species that are only recorded as naturalized in Australia and that have not been recorded as introduced in either ATSC or GBIF, this gave 924 records that state a species is a ‘weed’ or a similar synonym. We have assumed that the presence on this list is evidence of naturalization (i.e. escape from cultivation and self-sustaining population) and that if a record states a species is ‘invasive’, then it is.	Randall (2002) and May 2010 update of Global Compendium of Weeds supplied by R.P. Randall.	
South Africa	South African Herbarium records	Number of introduced species	69 (A2–E)	747 herbarium records of plants as part of a cultivated plant collection. Lists edited as for the global list.	H. Glen (pers. comm. 2009).
	Experimental forestry introductions	Success of introduction	3 (B2) 11 (B2–E) 5 (C3–D2) 12 (E)	Records of historical forestry trials for southern Africa. Many of these species may no longer be present (and so A2). Provides an indication of species, location, and result of introduction, but it is known to not be a complete list, e.g. it does not include <i>A. implexa</i> , and some errors have been identified, e.g. <i>Acacia paradoxa</i> is much more widespread than recorded (Zenni <i>et al.</i> , 2009).	Poynton (2009).
	Southern African Plant Invaders Atlas (SAPIA)	Number of naturalized or invasive species	1 (C3) presumed A2) 2 (C3) 2 (D1) 14 (E)	Record of the species outside of cultivation with the following updates: <i>Acacia cultriformis</i> has not been confirmed and is not included here; <i>Acacia fimbriata</i> is recorded as naturalized and a herbarium sample was taken several decades ago, but no plants are now present at the site (so presumed A2); A few plants of <i>A. retinodes</i> and <i>A. ulicifolia</i> are persisting and recruiting at Tokai Arboretum (C3), <i>A. viscidula</i> and <i>Acacia adunca</i> have naturalized and shown some propensity for local spread (D1), all other species show significant spread and recruitment beyond the point of introduction (E).	Southern African Plant Invaders Atlas (accessed March 2009) also J. Wilson pers. obs. 2011.

Each list is related to the different stages in the unified framework for biological invasions using the A–E scheme proposed by Blackburn *et al.*, 2011 (see the legend to Fig. 4 for a definition of the categories). Lists from South Africa were included in addition to the global lists as an example of regional application of lists. For further details and the actual data see Appendix S1.

Phyllodineae, only 17–20 species have native ranges that extend outside Australia, and only 10 are exclusively extra-Australian (Table 1), confined to the Indo-Pacific region. Within Australia, the east–west divide acted as an important evolutionary force because similar climatic and edaphic conditions occur on both sides of the Nullabor Plain. For example, Mediterranean-type climates occur in both south-western Western Australia and in South Australia, but only about 50 *Acacia* species have natural ranges that include both regions. Acacias are found in almost all habitat types across the continent and, together with eucalypts, epitomize the Australian landscape. The onset of aridity (c. 15 Ma), together with old and nutrient-poor soils, and complex interactions with climatic fluctuations and fire across much of the continent have stimulated a rapid radiation of unique adaptations in both acacias and eucalypts. For acacias, centres of high species richness, such as the Mediter-

ranean-type climate zone of the south-western corner of Western Australia (Fig. 1), have been foci of recent evolutionary divergence and also act as refugia favouring the persistence of some relict forms (Hopper & Maslin, 1978).

Possibly the most characteristic trait of many members of the group is the presence of persistent evergreen phyllodes (modified petioles) – scleromorphic features with various xeromorphic mechanisms. Sister lineages of *Acacia* subgenus *Phyllodineae* have bipinnate leaves, and the modified phyllodes appear to be a basal trait that was subsequently lost on at least three independent occasions (Murphy *et al.*, 2003). Phyllodes are highly variable in the group, differing in size, shape and nervation. These evolutionary changes are complex, and homology among phyllode variants is not well understood. However, it is hypothesized that phyllode architecture has been selected through changing environmental conditions,

specifically the change from mesic to arid landscapes. Like many leguminous species, all Australian acacias are thought to have a symbiotic association with rhizobia, which allows them to fix atmospheric nitrogen. The vegetation of Australia is unusual in that nitrogen-fixing plants, particularly acacias, are major components of most vegetation types. Some acacias combine fungal ectomycorrhizae and bacterial symbionts to assimilate nitrogen. *Acacia* species have particular pollination syndromes with low energy allocation to floral nectar but with high pollen rewards. Acacias have polyad pollen grains to maximize seed set after pollination. Other adaptations that have arisen as a consequence of this adaptive radiation are a suite of mechanisms to survive and persist fire (e.g. fire-

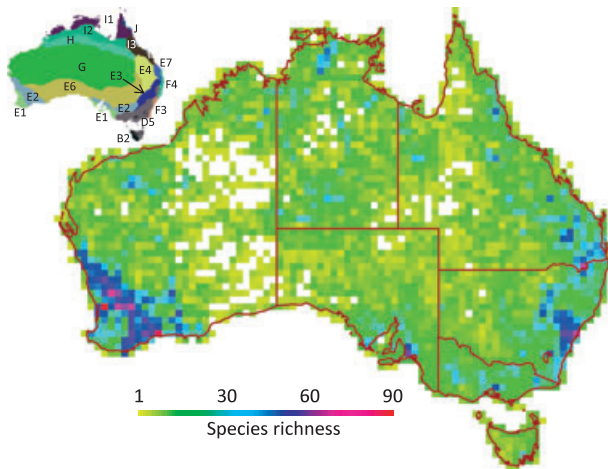


Figure 1 Species richness of Australian *Acacia* species across Australia (shading indicates number of taxa in half-degree cells). The inset shows the main categories of Australian agro-climatic classes (Hutchinson *et al.*, 2005). Major categories indicated on the map are: B (cold); D (cool wet); E (warm, seasonally wet/dry); E1 is classic 'Mediterranean' climate, E2 is 'Mediterranean'-type climate, but with drier cooler winters and less growth potential than in E1; F (warm, wet); G (warm to hot, very dry); H (hot, dry); I (hot, seasonally wet/dry); and J (hot, wet).

stimulated germination of soil-stored seeds, and resprouting) and, in some species, the utilization of animals for seed dispersal (elaiosomes to attract ants and arils to attract birds) (O'Dowd & Gill, 1986; Orians & Milewski, 2007). These features might explain the diversity and dominance of *Acacia* species across such a range of environments in Australia (Fig. 1).

Human-mediated transport of species beyond their historical ranges, especially in the last century, has breached biogeographical barriers *within* Australia, allowing many acacias to occupy novel habitats where some species have become naturalized or invasive (*sensu* Pyšek *et al.*, 2004), changing the continental-scale distribution pattern of the genus. At least 11 species are classified as invasive within Australia (Richardson & Rejmánek, 2011) and many more are established/naturalized outside their natural ranges. Within Australia, the ranges of some acacias have altered with human activities. Land transformation through agriculture and urbanization has not only led to range reductions but also to expansions, thus altering the dynamics of Australian acacias even within Australia.

THE JOURNEY: AUSTRALIAN ACACIAS ON THE MOVE (THE GEOGRAPHIC BARRIER)

Whereas most intercontinental movements of plants in the colonial era was from the 'Old World' to the 'New World', Australian acacias and eucalypts represent a special case in 'ecological imperialism' (Crosby, 1986). Species from both groups became conspicuous, even dominant components in many regions of the world soon after they were introduced and widely planted. The export of Australian acacias to other parts of the world began soon after the arrival of Europeans in Australia in 1788. Many Australian acacias were growing in Europe by the end of the first quarter of the 19th century (Cavanagh, 2006). Kull & Rangan (2008) provide a succinct summary of the main phases of the dissemination of Australian acacias around the world. They separate four groups of Australian acacias in the 'Outbound from Australia' compo-

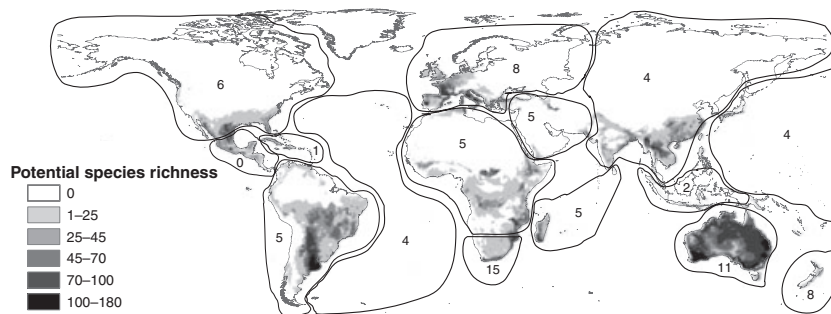


Figure 2 The number of invasive Australian *Acacia* species known in each of 15 regions of the world (Richardson & Rejmánek, 2011) and a map of areas climatically suitable for Australian acacias. Shading indicates number of species that could potentially grow in different areas. Results are based on a bioclimatic analysis using a simple envelope approach using all taxa of Australian acacias from Australia's Virtual Herbarium (2010) with six or more records (838 species were used to produce the map). Methods used in generating the map are described in Appendix 2.

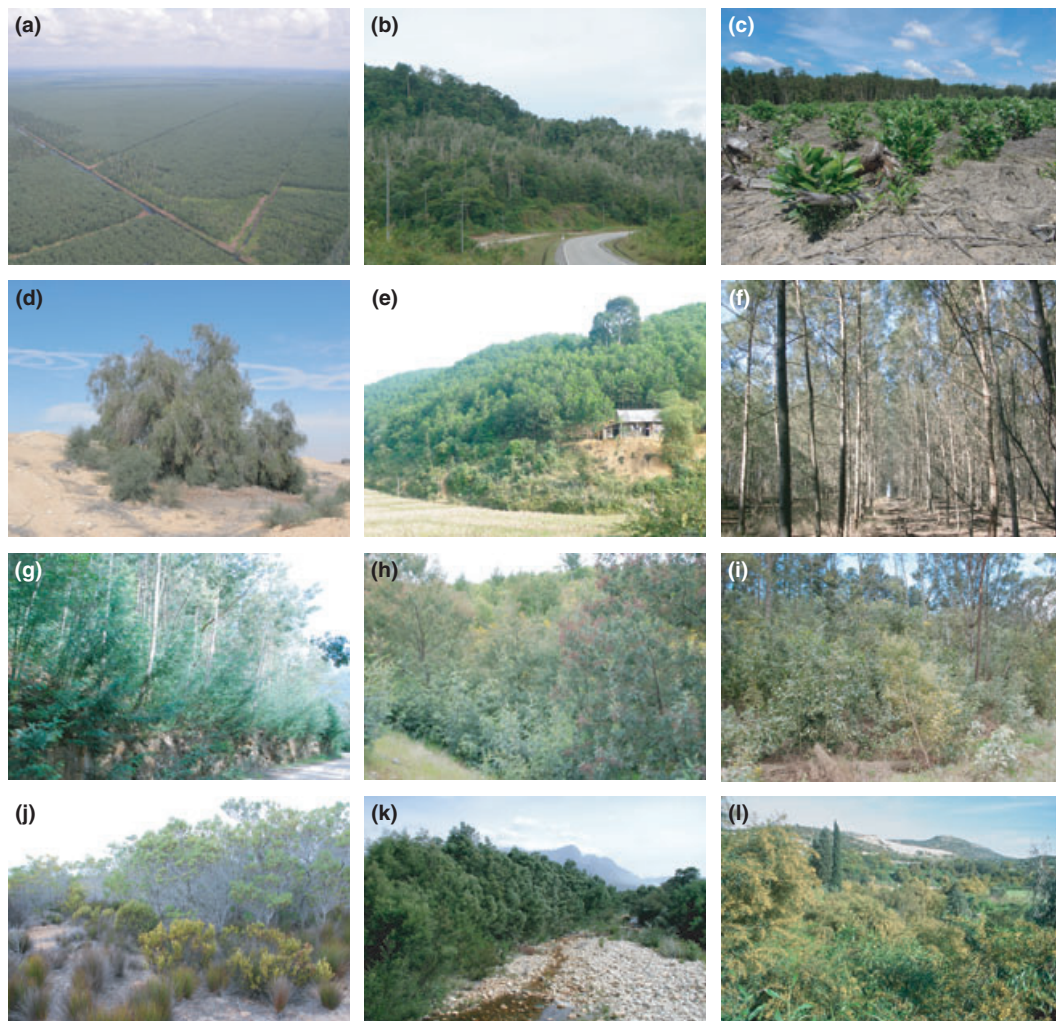


Figure 3 Examples of landscapes in different parts of the world dominated by Australian acacias. (a) Plantation of *Acacia crassiparpa* in Riau Province, Sumatra (photograph: S.J. Midgley); (b) Derelict *Acacia mangium* plantation (foreground) with undisturbed tropical dipterocarp forest in the background in Sampadi, Lundu district, Sarawak, Malaysia (photograph: B. Bakar); (c) *Acacia mangium* plantation in Sumatra, Indonesia (photograph: M.J. Wingfield); (d) Self-sown *Acacia salicina* growing in the Negev desert, Israel (photograph: J.-M. Dufour-Dror); (e) A natural hybrid of *Acacia auriculiformis* and *A. mangium* growing on previously bare and overgrazed land between Vinh and Hanoi, Vietnam (photograph: S.J. Midgley); (f) Commercial *Acacia mearnsii* plantation in KwaZulu-Natal, South Africa (photograph: G. Chigeza); (g) Invasive *Acacia dealbata* near Coimbra, Portugal (photograph: D.M. Richardson); (h) Invasive *Acacia dealbata* near Concepcion, Chile (individual with pods in right foreground) (photograph: D.M. Richardson); (i) Mixed stand of invasive trees in the Western Cape, South Africa, with *Acacia pycnantha* in the foreground (photograph: D.M. Richardson); (j) *Acacia cyclops* invading fynbos vegetation, Western Cape, South Africa (photograph: D.M. Richardson); (k) *Acacia mearnsii* invading riparian vegetation, Western Cape, South Africa (photograph: D.M. Richardson); (l) *Acacia saligna* invading near Skarinou, Cyprus (photograph: C. Christodoulou).

ment of world-wide ‘acacia exchanges’: cool-climate wattles; *Acacia melanoxylon*; tropical acacias; and arid-zone acacias. Besides the different species involved in these exchanges, the four groups differ importantly in terms of the agencies responsible for intercontinental, regional and local movements. South Africa received a greater diversity and magnitude (in terms of numbers of introduction events and total propagule pressure) of Australian acacia introductions than any other region in the 19th century. About 70 species were introduced, most of them in the mid-19th century (Poynton, 2009; Table 1). Another major boom in introductions and plantings

to additional countries outside Australia occurred around 1980 (Griffin *et al.*, 2011).

Details on introduction histories of alien species are important for understanding many aspects of their performance in new environments. Although (putative) dates of introduction and other aspects, such as approximate number of seeds and likely provenance, are available for some species (e.g. Poynton, 2009), data are sparse for most species and the reliability of available data is questionable in some cases. Molecular techniques provide exciting opportunities for enhancing our understanding of mechanisms underlying

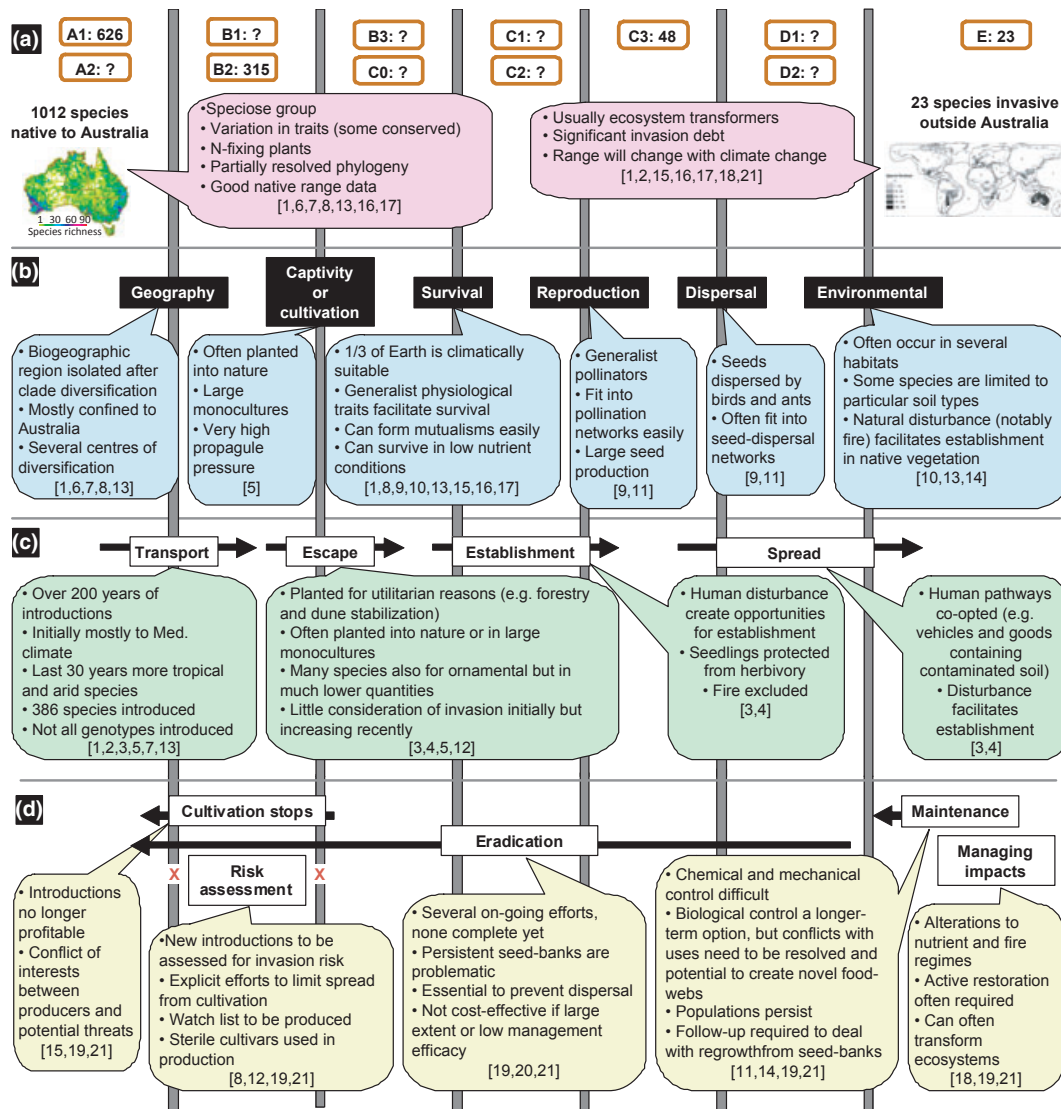


Figure 4 Key issues emerging from Australian acacia introductions as a natural experiment based on the papers in this special issue. These papers are mapped onto relevant points of the proposed unified framework for biological invasions (adapted from Blackburn *et al.*, 2011). The numbers in square brackets refer to the papers in the species issue (see below). (a) The number of species in each introduction category (i.e. the state) based on Tables 1 & 2. The full data are in Appendix S1 (see below for the definitions of the categories); (b) The biotic and abiotic barriers to invasion; (c) How humans have facilitated the process of Australia acacia movements and invasions; (d) Management actions. *Category definitions*: A1: no individuals transported beyond limit of native range; A2: historically transported but no longer found outside Australia; B1: individuals transported beyond native range and kept in captivity or quarantine; B2: individuals transported beyond limits of native range, and in cultivation; B3: individuals transported beyond limits of native range, and directly released into novel environment; C0: individuals released into the wild in location where introduced, but incapable of surviving for a significant period; C1: individuals surviving in the wild, no reproduction; C2: individuals surviving and reproducing in the wild, but no populations self-sustaining; D1: self-sustaining population in wild individuals dispersing a significant distance and surviving; D2: as D1, but individuals also reproducing a significant distance from the parent plant; E: invasive across several habitats. *References*: [1] This paper; [2] Richardson & Rejmánek (2011); [3] Carruthers *et al.* (2011); [4] Kull *et al.* (2011); [5] Griffin *et al.* (2011); [6] Miller *et al.* (2011); [7] Le Roux *et al.* (2011); [8] Hui *et al.* (2011); [9] Gallagher *et al.* (2011); [10] Morris *et al.* (2011); [11] Gibson *et al.* (2011); [12] Castro-Díez *et al.* (2011); [13] Rodríguez-Echeverría *et al.* (2011); [14] Veldtman *et al.* (2011); [15] Wingfield *et al.* (2011); [16] Webber *et al.* (2011); [17] Thompson *et al.* (2011); [18] Le Maitre *et al.* (2011); [19] Wilson *et al.* (2011); [20] Moore *et al.* (2011); [21] Van Wilgen *et al.* (2011).

successful invasions by shedding light on key facets of introduction histories, such as the number of introductions (single versus multiple – shown to have profound implications for performance), the relationship between genetic diversity of

introduced species and their performance, the occurrence and extent of hybridization within or between species, and the identification of native provenances (Le Roux & Wiczorek, 2009). Elucidation of subsequent processes and the fate of

introduced species rely on the availability of accurate data on the extent to which species in a given group have been introduced to new regions and have had sufficient time to 'sample' new habitats. Table 1 shows the rich data available for exploring the reasons for the number of Australian *Acacia* species at different stages of the introduction-naturalization-invasion continuum in different parts of the world.

ARRIVING: HOMES AWAY FROM HOME

Most Australian acacias were transported to foreign environments as seeds and in some cases (e.g. in South Africa) in very large numbers that were immediately sown into natural ecosystems for specific purposes. Considerable care was sometimes taken to nurture young plants to protect them from competition from native plants and various other factors such as herbivory. In the case of commercially important agroforestry species, natural vegetation was cleared to remove competing native species. Many species were intentionally very widely disseminated by humans in new regions, rapidly creating large seed pools at multiple foci. The many ways in which Australian acacias were welcomed and nurtured in their new homes and the needs that they satisfied were crucial for determining subsequent trajectories of performance, abundance and distribution, as well as their impacts on ecosystems and the extent to which they were welcomed or detested by human societies.

Australia has a wide range of environments and bioclimatic zones. Figure 2 shows that roughly a third of the earth's land area has bioclimatic conditions similar to those that exist within the native ranges of Australian acacias. This is the template upon which most introductions have taken place. Among regions that have received imports of Australian acacias, perhaps none is more suitable in terms of broad-scale bioclimatic conditions than South Africa. All of South Africa's seven biomes have equivalent bioclimatic zones in Australia, and Australia has more than four times the land area with South Africa-like climate than exists in South Africa (Richardson & Thuiller, 2007). Broad-scale climatic matching is widely recognized as a fundamental requirement for the success of introduced plants. It is thus not surprising that all regions where Australian acacias are listed as invasive (Richardson & Rejmánek, 2011) were identified as being bioclimatically equivalent to areas within the range of a large number of Australian acacias (Fig. 2). No other region has more invasive Australian acacias than South Africa (Richardson & Rejmánek, 2011).

How invasive species interact with native biota is an important focus area in invasion biology. Among the key questions are: how does competition with native species influence community structure; and how do introduced species infiltrate seed dispersal and pollination networks and food webs? For legumes that form associations with nitrogen-fixing bacteria, a crucial issue is whether introduced species can form novel associations with native bacteria or whether they rely on compatible symbionts from the native range (Richardson *et al.*,

2000a). Despite the wealth of literature available on native-invasive interactions, surprisingly little is known about these aboveground-belowground interactions that are clearly vital mediators of the fate of introduced species (Bardgett & Wardle, 2010). Only very recently have researchers started to explore whether successful establishment depends on the degree of promiscuity; in other words, whether the ability to form associations with a wide range of bacteria is associated with wider environmental tolerance. Even a decade ago, almost nothing was known about these issues for introduced acacias (Richardson *et al.*, 2000a). Much work has been performed in recent years (Rodríguez-Echeverría, 2010), but many questions remain to be answered before a predictive understanding of this aspect of the biology of Australian acacias, and legumes in general, can be incorporated into models for predicting how different species will fare in different foreign environments (Rodríguez-Echeverría *et al.*, 2011).

THE CYCLE OF LIFE: REPRODUCTION AND DISPERSAL

Traits related to reproduction and dispersal are crucial for naturalization and invasion of species in new environments. Substantial advances have been made recently in understanding the links between particular traits and invasiveness of plants. Three main approaches have been followed in examining this issue: alien-alien congeneric comparisons, alien-native congeneric comparisons and multispecies studies. Each approach has its advantages (Pyšek & Richardson, 2007), but detailed studies of congeners are probably the most powerful approach (Richardson, 2006). Although the large number of taxa of Australian acacias is attractive for such studies, a major hurdle in this group is the shortage of data on many species, especially those that have not been widely introduced around the world and/or that are not of special importance to humans. Despite this problem, important opportunities exist to contrast levels of success as introduced species with different traits. This is important, since information on traits is widely used in screening protocols to identify species with a high risk of becoming invasive (e.g. Tucker & Richardson, 1995).

HERE TO STAY? THE HUMAN DIMENSION OF INTRODUCED ACACIAS

Several features of Australian acacias make them important to humans. The foliage, seeds, wood and bark of many species have been used by humans for centuries as fodder for livestock, sources of famine food, medicines and fuel. The desire for these products has led to extensive human-assisted movement of some species to areas far removed from their native ranges. In particular, about a third of Australian acacias are trees, and several species are key components of agroforestry in the tropics (Richardson *et al.*, 2004a,b). Their rapid growth rates, ability to survive and flourish in nutrient-poor, arid or degraded sites and their dense wood make them sought after for different types of forestry in many parts of the world. Many

species also have attractive forms, floral displays or foliage, making them increasingly popular for ornamentation (Ratnayake & Joyce, 2010).

Together with the scientific importance of introduced acacias and what they illuminate in terms of dispersal, human-mediated introductions of Australian acacias also contain the history and expectations of both exporters and importers of the species. The exchanges and their effects thus raise fresh questions for historians, philosophers and social scientists. Their very introduction has polarized scientific politics around the human values of acacias in their home ranges in Australia (where they are of symbolic value) and the

places to which they have been introduced where, in some cases, having first been celebrated they later became demonized. Questions around the fundamental principles and philosophy of invasion biology are also germane to this global experiment. Historians have had to come to grips with the motivations (which have not always been strictly utilitarian) of introducing Australian acacias and with the economic benefits that have accrued from a variety of acacia products such as timber, fuelwood, perfume, food and animal fodder. Philosophers have also been encouraged by invasion biology and the acacia experiment to give close consideration to environmental aesthetics and a system of 'values'. Social scientists have

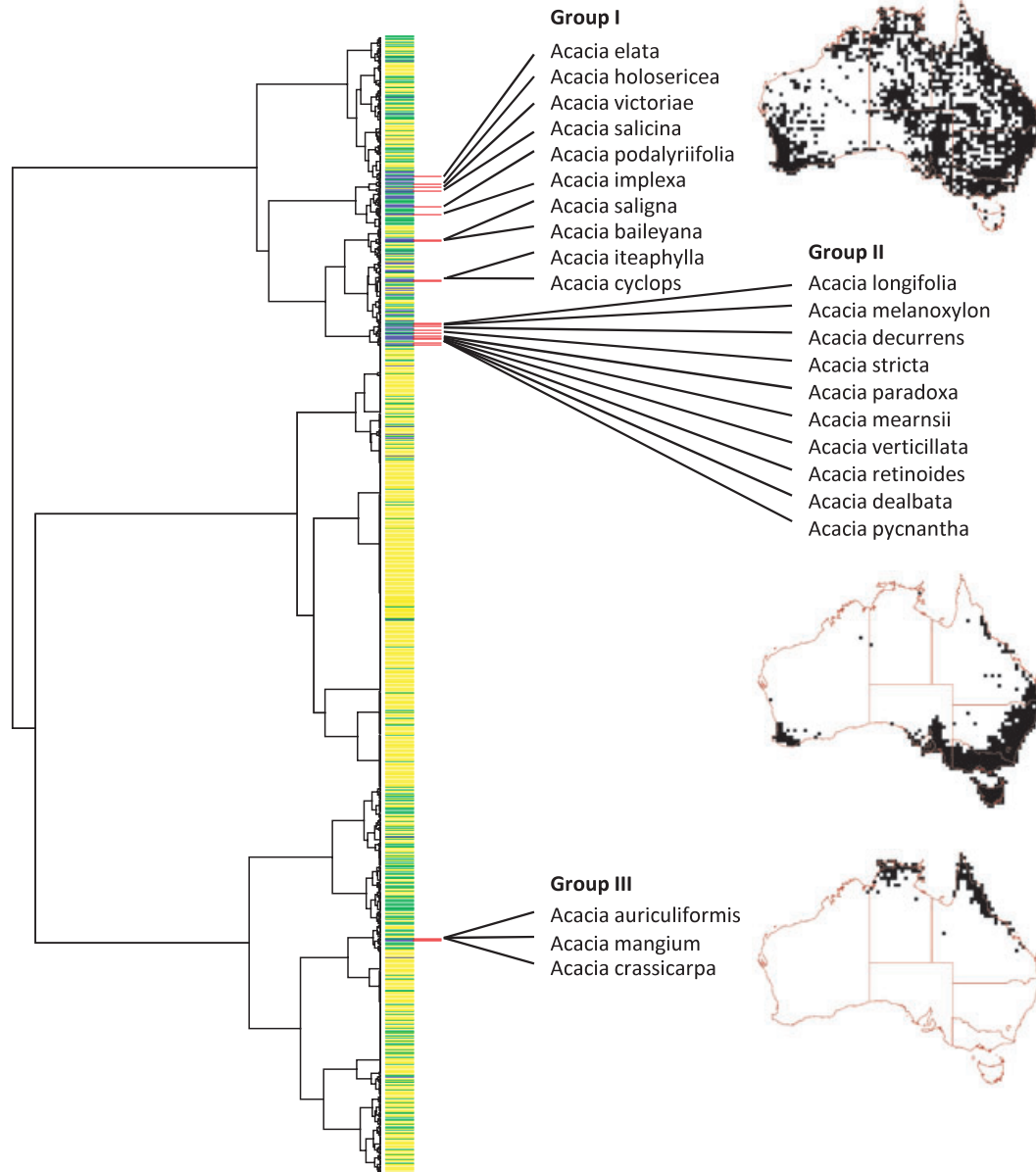


Figure 5 Cluster analysis with Ward linkage rule of the 1012 Australian *Acacia* species according to their occurrence (using records from Australia's Virtual Herbarium) in 18 Australian agro-climatic classes (Hutchinson *et al.*, 2005; see Fig. 1). Different subsets of species are colour-coded: (1) those not known to have been introduced outside Australia (yellow); (2) those introduced but not known to have naturalized (green); (3) those known to have naturalized (blue); and (4) 23 invasive species (Richardson & Rejmánek, 2011) (red). The three maps show the combined distributions of three groups of invasive species.

examined how these introductions have impacted on the culture and daily life of the people who use acacias in these different ways and how these relationships have changed over time. A range of ideas and perceptions relating to ecological restoration and the nature of science have also been uncovered by this global experiment.

CONCLUSIONS

The Australian environment and its evolutionary history have served as a factory for a highly diverse flora that is extremely well adapted for survival, growth and proliferation in many parts of the world that have, until recently, been isolated from Australia. The evolutionary milieu, has fortuitously also manufactured a bewildering number of plants that are, for diverse reasons, highly sought after by humans across the globe. These two factors, in intricate combination with complex socio-political and cultural histories, have designed the natural experiment that is the subject of this special issue of *Diversity and Distributions*. As with all natural experiments in biogeography and ecology, the design is imperfect. Among the imperfections are the following:

1. Species have not been moved out their native ranges to the same extent (in similar numbers and over equivalent periods) and many have not been moved at all, creating a biased set of species (Fig. 5), making it challenging to tease apart human factors from biological mechanisms as mediators of invasion success.
2. Traits associated with ecological performance and thus potential invasiveness in new environments are intricately linked with traits associated with usefulness of species to humans (neither set of traits maps evenly across the phylogeny or functional groups). This complicates attempts to separate proximate and ultimate explanations for different degrees of naturalization/invasion of introduced species, since propagule pressure may override and mask other contributing factors.
3. Accurate data on most traits is available for only a small sample of species in the group – for the most part only for those species that are most useful to humans (and a few taxa of special interest in their native range). This complicates attempts to correlate performance as introduced species with traits across the full spectrum of species.

Despite these caveats, the studies collected in this special issue demonstrate many innovative approaches for gaining important new insights into the many factors that influence: how and why Australian acacias have succeeded in expanding their range so dramatically in recent centuries; how their presence, distribution, abundance and interactions with resident biota and ecosystems are perceived by humans in a broad spectrum of social settings; and the options open for different forms of management in the face of complex human value systems and a rapidly changing environment (Low, 2011).

Although Australian acacias are already dominant components of many ecosystems outside Australia, scholarly reflection and scientific investigation of the natural experiment have only just begun. Pathways of transfer and dissemination

are changing continuously, as are the habitats and socio-political environments into which the species are being introduced. So too are the societies in which these species grow. Are some Australian acacias 'super species' (sensu Hamilton, 2010) that will increasingly dominate large parts of the planet? If so, how can we manage these species to maximize their potential usefulness while mitigating the damage that they cause to ecosystems in some regions and under certain situations? It is hoped that this special issue will serve as a catalyst for further studies that will provide the foundation needed to guide the objective management of Australian acacias in all the many environments where they now occur.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 A database of different lists of Australian *Acacia* species used to identify the introduction status of each species (as per Fig. 4; with some of the sources summarised in Table 1).

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BIOSKETCH

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APPENDIX 1 ACACIA THEN AND NOW – A BRIEF HISTORY OF THE TAXONOMY OF THE GROUP

The genus *Acacia* was originally described by P. Miller in 1754 from an African species (*Acacia senegal*), and early definitions included many species of Mimosoideae legumes that are no longer part of *Acacia sensu lato* (Miller, 1754; Willdenow, 1806; de Candolle, 1825). In a series of works in the mid-19th century, Bentham (1875) circumscribed Mimosoideae tribes and within it *Acacia*, diagnosed by having infinite free stamens, into the broad forms we know today. However, based on current knowledge of the group, there are no defining morphological characters that differentiate *Acacia sensu lato* from other genera of the Tribes Mimoseae and Ingeae (Maslin *et al.*, 2003). Pedley (1986), generally following Vassal's (1972) subgeneric classification, proposed that the genus be divided into three genera: *Acacia*, *Senegalia* and *Racosperma*. This work initiated investigations into *Acacia* to determine whether indeed *Acacia sensu*

lato was polyphyletic and what characters differentiated the putative segregate genera. A detailed overview of the generic history of *Acacia* is provided by Maslin *et al.* (2003).

The first molecular studies focussed on either the African or the American species but did not sample enough to determine broader relationships (Clarke *et al.*, 2000; Robinson & Harris, 2000). The first studies using DNA sequences that sampled more widely (Miller & Bayer, 2000, 2001) determined that the genus was polyphyletic, containing three distinct lineages broadly conforming to the Vassal (1972) and Pedley (1986) taxonomy. This was confirmed by larger studies of the Mimosoideae (Luckow *et al.*, 2003) and Ingeae (Brown *et al.*, 2008). A review of the molecular systematics of *Acacia sensu lato* is provided by Miller *et al.* (2011). This work showed that *Acacia* subgenus *Acacia* is embedded within Tribe Mimoseae and that the mainly Australian acacias of *Acacia* subgenus *Phyllodineae* are more closely related to a paraphyletic tribe Ingeae than to other species in *Acacia sensu lato*. Amid controversy (McNeill & Turland, 2010a, 2010b; Moore *et al.*, 2010), the type of the genus was changed from the African *Acacia nilotica* to the Australian species *Acacia penninervis* at the International Botanical Congress in 2005.

Acacia s.l. has three main centres of diversity. Both the Americas and Africa are home to *Acacia* subgenus *Acacia* (*Vachellia*) and *Acacia* subgenus *Aculeiferum* (*Senegalia*) while the large radiation of *Acacia* subgenus *Phyllodineae* is mainly found in Australia. Indeed, ~99% of Australian *Acacia* species belong to *Acacia* subgenus *Phyllodineae* (Table 1), and similarly, c. 99% of *Acacia* subgenus *Phyllodineae* are native to Australia. While *Acacia sensu lato* can be found in many environments it comprises a major component of arid and semi-arid zones in Australia, Africa and the Americas. With one exception, all *Acacia* species not assigned to *Acacia* subgenus *Phyllodineae* have bipinnate leaves. These species, including over 95% of the Australian species, have modified petioles called phyllodes. Other characters that are common but not found in all Australian *Acacia* species include extraporate pollen with a reticulate exine, inflorescences that are either simple or racemose with flowers arranged in globular heads or cylindrical spikes. Most often the inflorescences are golden yellow or creamish white.

Pedley (1978) developed a sectional classification of *Acacia* subgenus *Phyllodineae* that included seven groups based mainly on leaf and inflorescence characters. While the sections have not been considered natural groupings, they provided a convenient method of describing the vast diversity of the group. Two small groups contained only bipinnate species: *Pulchellae* from SW Western Australia and the *Botrycephalae* from SE Australia. Two other small non-phyllodinous groups, sections *Lycopodiifoliae* and *Alatae*, are found in Western and northern Australia. There are two main types of phyllodes those that contain a single main nerve (section *Phyllodineae*) and those with multiple nerves (section *Plurinerves* which has globose inflorescences and section *Juliflorae* with spicate

inflorescences). Together, these three sections comprise *c.* 90% of the species. Molecular systematic work is beginning to develop the basis for a phylogenetic-based classification of the genus (Murphy *et al.*, 2010; Miller *et al.*, 2011). While few if any of these taxonomic sections are monophyletic in molecular analyses, the phylogenetic patterns will help unravel character evolution of important reproductive traits (Gibson *et al.*, 2011) and traits that may allow a high level of invasiveness (Gallagher *et al.*, 2011).

The latest phylogenetic tree of *Acacia* identifies areas that require further taxonomic and genetic work based on poor resolution of relationships. The least resolved part of the tree contains the bipinnate and uninerved racemose species which are generally found in SE Australia (Fig. 3 in Miller *et al.*, 2011). This clade, which contains nine invasive species, is well supported but there is little resolution within it. Hybridization, lineage sorting and lack of taxonomic effort are probable reasons for this result, and it will require detailed genetic and taxonomic research to resolve.

APPENDIX 2 METHODS USED TO MAP POTENTIAL DISTRIBUTIONS OF AUSTRALIAN ACACIAS OUTSIDE AUSTRALIA

We used six interpolated bioclimatic variables (10 min spatial resolution) obtained from WorldClim (<http://www.worldclim.com>; Hijmans *et al.*, 2005) as predictor variables for developing simple climate envelope models for each species. These

variables included the following: maximum temperature of warmest month, minimum temperature of coldest month, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter.

We obtained a dataset of occurrence records for 1012 Australian acacias from Australia's Virtual Herbarium. To reduce spatial sampling bias, we retained only one occurrence record per 10 min grid cell for each species. We then excluded all species for which there were fewer than five independent records, leaving a total of 838 species for which potential distribution models could be developed.

For each species, we calculated the 1st and 99th percentile for values extracted from occurrence records for each predictor variable. These percentiles were used to identify the range of values that each species could tolerate for each predictor variable. We used this approach to minimize the effect of possible outliers that could have been present in the dataset because of misidentification errors. For each species, we reclassified each of the six predictor variable maps into a map consisting of presence (value = 1) or absence (value = 0), using the percentile values calculated for that species. We then multiplied these presence-absence maps to generate a final map indicating the potential distribution of that species. We added the potential distribution maps for all 838 species to generate a map of potential species richness. The analysis was conducted using R statistical software (v. 2.11, R Development Core Team, 2010).