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Review

Taming the wild and 'wilding' the tame: Tree breeding and dispersal in Australia and the Mediterranean

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ABSTRACT

The olive (*Olea europaea*) and the wattles (mimosas or *Acacia* spp.) are typical tree species of the Mediterranean and Australia, respectively. Both trees have been subject to trans-oceanic movements, including the introduction of Mediterranean olives to Australia, and the introduction of Australian wattles to the Mediterranean. In each case, the trees have naturalised and become problematic invasives. Based on case studies of such movements, we compare and contrast the processes of transfer, dispersal, and genetic changes of these trees, with particular attention to crop–feral–wild complexes in both their home ranges and in introduced areas. Contrasting ecological, social, and economic landscapes shape the possibilities for crop–feral–wild interactions and for invasiveness.

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1. Introduction

Some plants are crops and some are weeds, but a crop in one region may be considered a weed in another. This simple distinction is further complicated by the status of different plants as 'native' or 'introduced', their status as domesticated 'cultivars' versus 'wild' species, and the potential that cultivars escape and become 'feral' or that wild introduced plants escape and become 'invasive'. In some cases, cultivated plants and feral weeds of the same species occur in close proximity, whether in their endemic region or in places of introduction. Such crop–feral–wild complexes call for attention to the importance of *genetic* processes not just in crop productivity, but also in invasive species management. Most invasion biology – particularly in its management applications – focuses on the species level, not on sub-species botany. Understanding the genetic interactions of cultivated plants with feral and wild relatives, or understanding the genetics underlying a plant's propensity to prosper in new environments, will allow for better management of plant invasions and genetic-level biodiversity.

Here we review the agronomic, ecological, and socio-economic trends that together have changed the status of two emblematic types of tree (the olive and the acacia) that have been introduced to each others' native regions (respectively, the Mediterranean and Australia). We focus on these two regions, and not any of the other areas where these crop–feral complexes exist. These paired case studies allow us to compare and contrast the processes of transfer, dispersal, and genetic changes, and resulting impacts on genetic diversity and landscape invasion.

The two taxa represent strongly contrasting situations, yet both simultaneously serve important economic functions, are culturally celebrated, and have resulted in problematic invasions of uncultivated land. The long-lasting and slow-growing domesticated olive, which has been shaped by humans for many millennia but still interacts with its wild and feral forms, has surprisingly escaped from cultivation in Australia. Less surprisingly, the fast-growing, short-lived acacias – only cultivated for the past two centuries – have also escaped from gardens and plantations in the Mediterranean. We hope that these two invasive/crop models will help to understand similar situations for other feral–weed–crop complexes.

1.1. Crops, weeds, ferals, and invasives: concepts and terminology

The terms used to discuss plant introductions, domestication, and ferality have been the subject of much discussion [1,2]. We use the following terms. *Crops* are the produce of intentional cultivation of plants. Many *cultivated plants* no longer resemble their wild relatives due to human intervention in the biological evolution of the plants via breeding and selection. Most cultivated plants cannot maintain their populations if abandoned, or naturalise outside of crop fields or gardens. Constant human intervention is usually necessary for their survival [3]. *Weeds*, in contrast, are any undesirable plants in a particular agro-ecosystem; by definition these plants thrive without direct human aid. In most cases, the potential for weedy behaviour is neither detectable in the species' life history nor in its reproduction traits. Both autogamous and out-crossing species may behave as weeds.

Most cultivated crop plants – and many wild plants – have gone through the processes of *introduction* to new environments typically through human effort. Humans have been an important vector in the spread of plants since prehistoric times, both intentionally and unintentionally [4]. This accelerated with the development of trans-oceanic sailing capabilities. Humans move useful plants (food crops, forestry trees, medicinal plants, and ornamentals) as well as weeds. The plants targeted for transport have generally been domesticated plants that have undergone some prior breeding or selection for superior strains, but other species have been transferred unintentionally. Since the late 18th century, significant numbers of non-domesticated (wild) plants were moved for scientific and botanical purposes; some of these plants later underwent selection and domestication in their host environments. Plant introductions have necessitated distinctions between the *native* flora of a region and *exotic* or alien plants which are those plants that come from outside a particular region [5].

Once successfully introduced and cultivated in new environments, introduced crop plants sometimes 'go feral'. *Feral* plants are progenies of cultivars that have escaped from cultivation in agro- or natural ecosystems and exist as partially wild. They disperse through non-human vectors and reproduce without human aid [1]. In essence, feral plants are a subset of *naturalised* plants, which are all introduced species (in cultivar or wild form) that have established and propagating populations without conscious human intervention. A species is described as naturalised if it is self-sustaining [6].

Invasiveness is the ability of a plant to spread beyond its site of introduction and become established in new locations, particularly in natural or semi-natural environments, where it may have deleterious or beneficial effects on organisms already existing there, including pollinators, parasites, and grazers. There currently is a high level of concern about 'invasive alien' plants, though European concern lags behind places such as Australia [6,7].

Of particular interest to this paper is when cultivated plants grow in proximity to their feral and/or wild relatives. We call this *crop–feral–wild complexes*. The introduction of individuals from wild species can aid in the maintenance of biological diversity of useful crops. This was already noted by botanists [8] and used to justify the choice of wild species cultivated in the closed spaces of botanical gardens. In their area of origin most domesticated plants occur as crop–weed–wild complexes that may influence each other by means of introgression [1]. Few domesticated plants thrive independently of humans; those that do sometimes multiply through processes that are absent in the wild forms [9]. Humans have unintentionally modified the sexuality of the wild forms through breeding and selection because they have screened severely at each generation for recessive traits that appear preferentially when crops are self-compatible [10]. Self-pollination is not favourable for many out-crossing species as seeds or biomass yields may be affected by inbreeding depression (gene expression of negative recessive traits, resulting in physiological depression). In a crop–feral–wild complex recurrent gene flow between partners could favour the feral stages that accumulate alleles from the successive cultivars and these may become more competitive than the crop or the genuine wild form.

Crop–feral complexes, where cultivated and feral plants coexist and cross-hybridize, may become established and problematic even when far from their centre of origin. In California, for example, one finds a sugar beet/weedy beet complex, a wheat/oat complex, and a wheat/rye complex (all from Europe) as well as a sorghum sp. complex (from Africa). Conversely, several crop species from North America that have been introduced in Europe and other world areas for feeding people or animals behave as weeds or were accompanied by wild species as weeds. Examples include wild sunflower (*Helianthus annuus* L.) [11], *Helianthus petiolaris* or prairie sunflower [12] and *H. argophyllus* or silver sunflower [11], which accompanied cultivated sunflower (*H. annuus*) seeds in Europe, Argentina and Africa, and China. Weedy sunflower in Europe displays wild traits suggesting that contaminating seeds from wild sunflower of the States have been introduced with the crop [11].

1.2. The case-study species: botany and overview

1.2.1. Olive

The genus *Olea* contains about 30 species split into three subgenera, *Tetrapilus*, *Paniculatae* and *Olea*, found in Asia, Australia and Asia, Africa and Europe, respectively. The subgenus *Olea* is divided into two sections. *Ligustroides* (about 10 species) and *Olea* (one species: *europaea*). Both thrive in the mountains of East Africa and in the Pacific Islands, and *Olea* is also found west of the Sahara, in the Macaronesian Islands (Canary and Madeira) and the Mediterranean basin (Fig. 1).

The cultivated olive and the oleasters are considered as two varieties of *Olea europaea* subsp. *europaea* by botanists. The main phenotypic difference between the two is that the flesh is thicker and the fruit is larger in most of the cultivated varieties. Oleaster (var. *sylvestris*) is a highly branched evergreen tree, ranging from 2 to 15 m in height [13]. Pollination occurs in spring and fruit ripens in autumn. Its habitat is clear, open forestland and it is native to most countries around the Mediterranean basin, both in the east and the west. The cultivated olive (var. *europaea*) has been introduced around the world into areas with Mediterranean climates, where it is used as a food source as well as to perpetuate the traditions of olive oil and Mediterranean cooking. Unpruned cultivated and feral olives may easily be confused with oleaster.

O. europaea subsp. *cuspidata* from Asia–Africa has been introduced in Australia and in some Indian and Pacific Ocean Islands and can cross-hybridize with the *europaea*. This subspecies has a longer, wider leaf than the cultivated olive and edible drupes that are smaller and rounder than fruits from the oleaster [14]. This subspecies is generally used for windbreaks rather than a food source due to high levels of bitterness in the fruit.

Botanical keys made from voucher samples may not reflect the whole diversity of the wild and cultivated olives. Moreover, feral olives from Australia have not yet been described botanically.

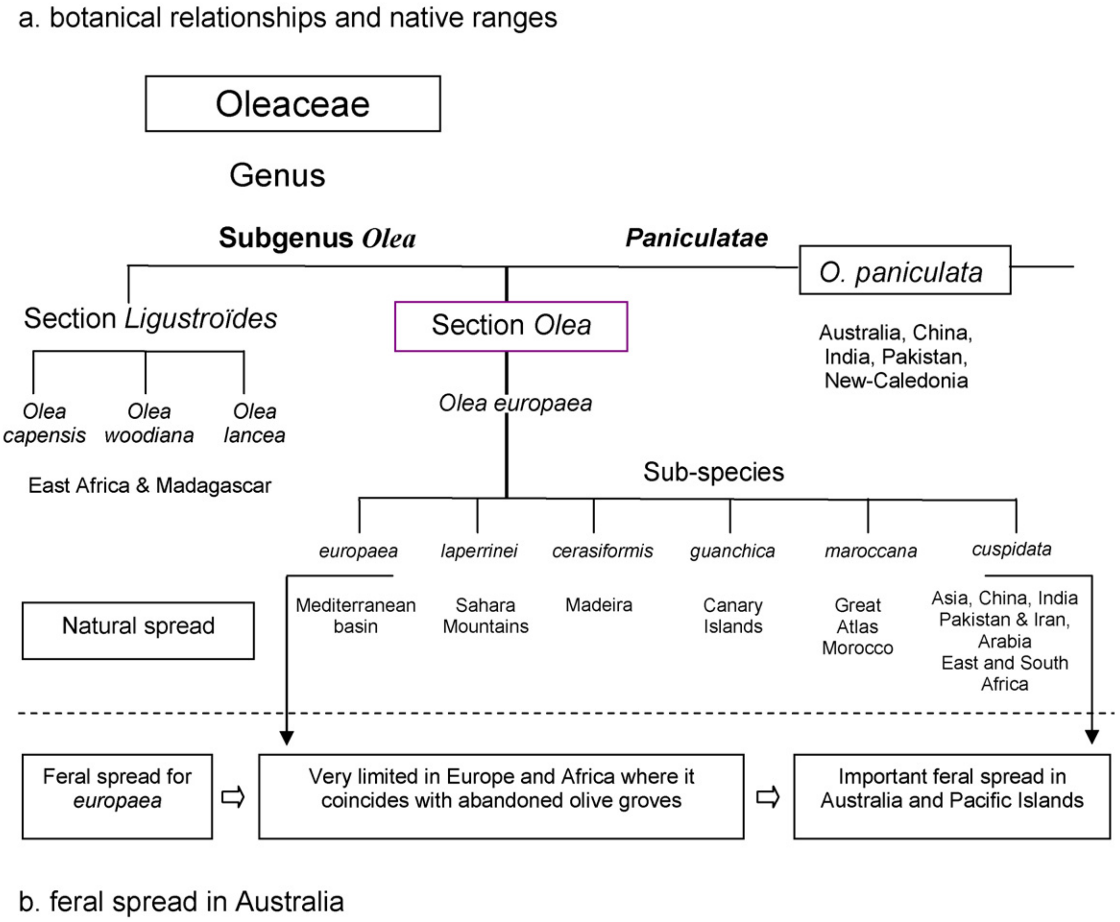

Fig. 1. (a) Botanical relationships and natural and feral geographic spread of *Olea* species, (b) feral spread in Australia. The arrows indicated species that spread.

Relationships between introduced and European cultivars remain to be established.

Cultivated olives coexist in much of the Mediterranean with their wild relative, the oleaster. Cultivated olives have long been dispersed and acclimatised to new areas by humans. New producer countries include Argentina, South Africa, and Australia. An olive industry has been established in Australia for over a century now, with the unintended consequence of a significant population of invasive feral olives [15–17].

1.2.2. Acacia

The genus *Acacia* (*sens. lat.*) (*Mimosoideae, Fabaceae)* includes over 1350 species around the world. Nearly 1000 are native to Australia. None are native to Europe. Acacias, which are often known as 'wattles' in Australia, are typically called 'mimosa' in Europe (confusingly, in Europe the unrelated plant *Robinia pseudoacacia* is commonly known as 'acacia') [18,19] (Fig. 2) Acacias come in extremely diverse forms, from pronate bushes to 30-m trees, and are unified by showy yellow flowers. Bipinnate leaves give way to phylloids in many mature Australian species.

Today, a number of Australian acacias have become naturalised across the Mediterranean basin, including mainland and island portions of Portugal, Spain, France, Italy, and areas of North Africa. Of chief concern to this review is the presence of 11 species of Australian acacias in the Mediterranean basin [20–22]. These include both bipinnate wattles (*A. dealbata, A. decurrens, A. mearnsii*, and *A. baileyana*) and phyllodinous wattles (*A. saligna, A. melanoxylon, A. retinoides, A. cyclops, A. pycnantha, A. sophorae*, and *A. verticillata*).

Australian acacias have been selected and bred for a variety of uses, including industrial forestry, agroforesty, and as ornamentals. In Australia a key role has been played by CSIRO's Australian Tree Seed Centre and other government agencies [23,24] in Europe, garden industries play a key role, particularly in breeding a number of popular ornamentals.

2. Natural history and introduction of olive and acacias

2.1. Olive

2.1.1. A short history of the olive in the Mediterranean basin

The phylogeny of *O. europaea* has not been completed and it is not possible to cluster accurately subsp. *europaea* in comparison to other subsp. Climate changes in the Tertiary period allowed the ancestors of *O. europaea* subsp. *cuspidata*, to spread towards the Mediterranean basin, the Sahara and the Macaronesian islands where they probably differentiated as diverse taxa [25]. Unfortunately, palaeobotanical evidence is insufficient to classify the taxa from ancient remains [26–28].

The distinction between a crop and its wild form, as for other plant species, is based on several criteria based on architecture and fruit size and, recently, pulp oil content [29]. Botanists have attributed the origin of the olive to the Fertile Crescent from subsp. *cuspidata* [30,31]. Geneticists and biologists have disagreed over the history of the cultivated olive. Geneticists have recognized its origin in the oleaster (subsp. *europaea*) based on molecular data [32–34]. We cannot exclude that crosses occurred between the two subspecies in the Iranian mountains, where *cuspidata* and the olive may have cohabited and that their progenies were introduced to the Fertile Crescent.

Consumption by humans began around 7000 years ago starting in the Fertile Crescent [35–37]. Archaeological data in Spain shows olive tree exploitation from about 6000 years ago [38,39]. The origins of olive domestication remain poorly documented. The first remains that are clearly from domesticated trees date around −5200 BP. Further evidence that human migration displaced cultivars toward the West [40] was derived from pit morphology [28]. These origins cannot be arranged chronologically without additional archaeological evidence. The origins of olive domestication have been reconstituted based on the molecular diversity found in present olive cultivars [41], but accurate dating is

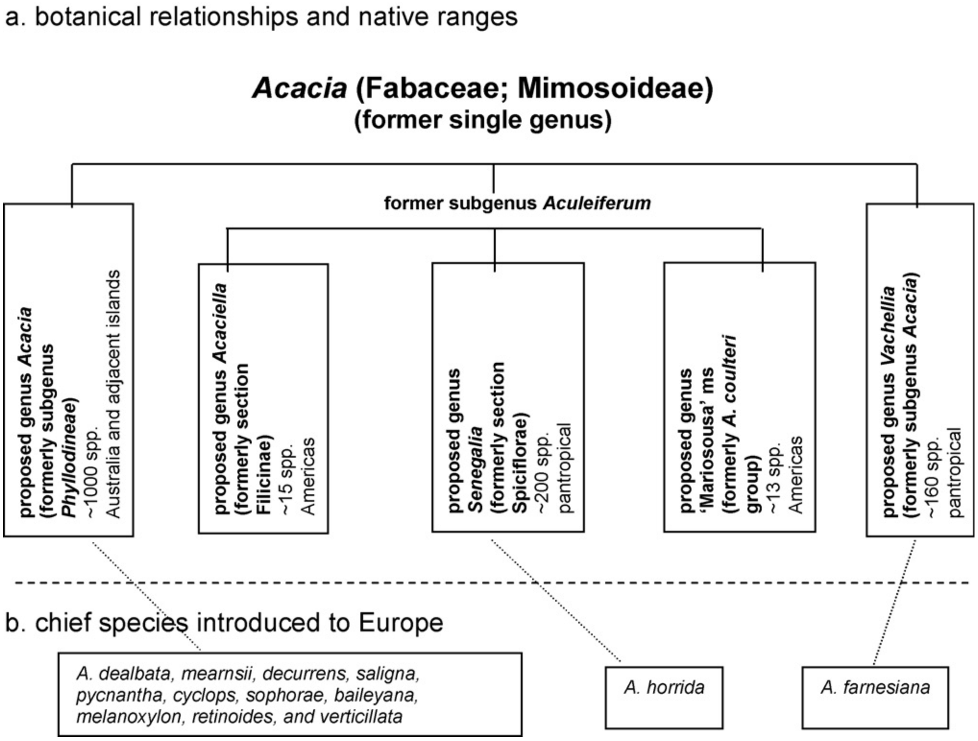

Fig. 2. (a) Botanic relationships and native ranges of acacias [Maslin 2007]; (b) main species introduced into Europe.

controversial, and for botanical ranking of partial specimens description is insufficient to enable comparison with modern olives. We can suppose that those cultivars domesticated in western regions have not diffused to the East. Other origins of domestication have been suggested in Tunisia–Algeria, Corsica, Morocco, Italy, Palestine, and France because cultivars share genetic relationships with local oleasters of these regions. Consequently, most cultivars may share origins at several times and places of domestication, as shown for 40 cultivars [41]. Human migration within the Mediterranean basin has resulted in dispersal of olive cultivars, but this movement is difficult to trace. Seed propagation loses the original variety, whereas cuttings maintain the cultivars, and probably both methods of propagation have occurred [42].

The present genetic identity of olive cultivars has been maintained for several centuries now, showing that they have not intermingled with other trees in their original environment. Once transported to new worlds they have met new environmental conditions as has occurred in Australia and the USA where trees have spread without the aid of human cultivation. Consequently, a new range of diverse individuals has been generated that do not exist in the Mediterranean basin. This is suggested by a study showing that molecular data from feral trees collected from Australia did not admix with European olives using Bayesian methods [27].

Domestication of the European olive has been described as partial since the feral forms thrive and multiply without human aid [27]. Olive cultivars are more widely distributed than the wild form [43], but feral olive trees are frequent in and around orchards. In some areas, cultivar–feral–wild olives live together within a radius of a few meters and they are not easily distinguished. Where the wild form is lacking in the environment, feral forms are identifiable, but they may be confused with the wild form [27].

The olive and oleaster spread in thermo-Mediterranean and meso-Mediterranean climates characterized by deep drought during summer. The olive must be watered in arid climates. In contrast subsp. *cuspidata* is found in a variety of different climates: arid in Yemen and humid in the highlands of India and East Africa. The adaptation flexibility of this subspecies may increase its invasive potential. Subsp. *cuspidata* is used as windscreen and its wood is used for charcoal in different countries. The fruits are not consumed due to their bitterness and poor oil content.

2.1.2. A short history of the olive in Australia

The impetus to start an olive industry in Australia was driven by the recognition that the soil type and climate, especially in Southern Australia, would be suitable for olive growing. Adelaide is located at latitude of 35°S, which is roughly equivalent, in the northern hemisphere, to Tunis in Tunisia. *O. europaea* subsp. *europaea* first arrived in Sydney in 1800 and *O. europaea* subsp. *cuspidata* was brought in about a decade later to be trialled as a rootstock [44]. Over 60 cultivars were imported to develop the new industry in New South Wales and South Australia [45].

Olives were planted during the 1800s in all states and territories except Tasmania. South Australia began to lead the industry by the 1830s and trees were subsequently imported from France, Sicily and Rio de Janeiro. French olive culture had a major influence on the South Australian industry. Methods of propagation, pruning and the majority of cultivars were sourced from France [46]. By the early 1900s approximately 83,000 trees had been planted in the state, which comprised the greater part of the industry at the time [47].

Despite suitable growing conditions the industry struggled to become commercially viable in its initial stages. The industry foundered and many groves became neglected in the 1950s. These groves – which covered an estimated 3000 ha in 1959 [48] led – to an abundance of olive seeds being distributed into surrounding areas. The resulting feral populations have made a significant impact on the South Australian landscape [15], spanning over 1000 km, predominantly within 400–600 mm median annual rainfall areas. Feral trees invading bushlands have reduced species diversity and altered of the canopy structure of the native vegetation, limiting the amount of light and inhibiting regeneration of native species [16].

The genetic diversity within the olive cultivars imported into Australia encompasses roughly 100 different genotypes. These genotypes are reproduced through clonal propagation and their number is unlikely to increase greatly unless many new cultivars are imported. However, the diversity within the feral populations would comprise thousands of different genotypes that did not fit European genetic classes [27], as each new seedling is derived from sexual reproduction and produces a genetically unique individual. The diversity of the feral populations, grown without any agricultural aid, could give rise to superior varieties for cultivation as well as individuals with increased weedy potential.

2.2. Acacia

2.2.1. A short history of acacia in Australia

The Australian continent has undergone a long-term trend of aridification, playing a key role in the radiation of Fabaceae, including acacias [49,50]. The 1000-odd species inhabit every ecological zone on the continent. Aboriginal Australians have relied on them for many thousands of years, eating the seeds of certain species and utilizing wood, bark and leaves for cooking, medicines, shelter, and tools. While Aborigines undoubtedly spread seeds and created ecological conditions for wattle propagation (e.g. through fire), modern seed selection and cultivation did not begin until the 1800s with the work of European botanical collectors (see next section) and – in the case of the economic species *A. mearnsii* (used for tanbark) – in reaction to overexploitation of wild stands.

During the late 19th and early 20th centuries, wattle flowers became widely used in domestic decoration and on ceremonial occasions, and different wattle species became favourite specimen trees in public and private gardens [51,52]. This stimulated significant horticultural development with the commercial supply of seeds and seedlings from private nurseries (including seed selection and hybridization). Nurseries and garden enthusiasts continue to breed for particularly or unusual or showy flowers and leaves. Gardening is known to have spread feral members of a number of species, such as *A. baileyana*, outside their native range in Australia [53].

Wild acacias play a small economic role in contemporary Australia. A number of species are exploited in the logging of native forests (often in mixed stands with eucalypts) for sale as pulp or construction wood. [20,54]. Such forestry facilitates the spread of some pioneer species like *A. decurrens*. Other species are harvested for uses such as fence posts, handicrafts, drought fodder, or ‘bushfoods’ [55], yet few attempts have been made at cultivation or domestication for these purposes.

2.2.2. A short history of acacias in France and the Mediterranean

The earliest documented transfers of Australian acacias to other continents occurred in the late 1700s with British and French exploration of the Australian coast [56,57]. Introductions increased in the mid 1800s, with botanic garden networks, ‘acclimatisation’ societies, and private enthusiasts moving large quantities of seeds for scientific, decorative, and economic goals [7,58]. Numerous Australian wattles now grow around the Mediterranean basin, as well as in California, South Africa, Madagascar, India, Brazil, and Hawaii [61,62]. These introductions have set the groundwork for work on seed selection and plant stock improvement, as well as attendant and unexpected invasions.

In France, interest was sparked by scientific curiosity, gardening enthusiasm, and the possibility of uses for economic ventures, soil stabilisation, and reforestation. Some 55 spp. of Australian acacias had been introduced in the botanic garden of Thuret in Antibes between 1858 and 1871 [63]. By the 1860 and 1870s, *A. dealbata*, the best suited species, was well established in southern France; it has since become invasive in some parts of the Côte d'Azur [7,20,22].

Breeding and selection effort has focused on *A. dealbata*, which has become important to both a cut flower industry and a perfume extraction industry [64,66]. The flower industry developed in the late 1870s when trains could speed the winter blooms to northern Europe [64,65]. These industries rely on harvests from ca. 250 ha of cultivated wattles (mainly *A. dealbata* × *A. baileyana* hybrids) [64] as well as from feral *A. dealbata* populations. Gardeners have created several new cultivars based largely on *A. dealbata*.

Other acacia species are also common. *A. melanoxylon* is both an ornamental, and used for timber in Portugal. *A. mearnsii*, a very important tanbark and pulpwood species in southern and eastern Africa (where it has been subject to breeding and selection for over a century [66]), is also present in the Mediterranean. *A. saligna* is widespread in North Africa, where it is used for environmental rehabilitation, dune stabilisation, fodder, and firewood. It was also introduced during the British mandate to Palestine to arrest sand dune movement. It became feral and a pest in many habitats. While many such acacias have become invasive, most are valued as ornamentals or for minor forest product exploitation [23,67,68].

3. Dispersal

3.1. Agents of dispersal

3.1.1. Olea

Mammals disperse olive kernels over short distances (meters). In contrast, seed dispersal by birds covers wider distances, depending on both the size of the birds and the size of kernels. At least 25 bird species can move olive kernels [44,69,70]. Seabirds such as yellow-legged gull (*Larus michahellis*) may displace olive kernels over several tens of km through pellets [71]. This may explain the long distance displacement and tight genetic relationships between distant wild olive stands, as has been found between Corsica and Spain or Corsica and Morocco [29].

The most common methods of olive spread within Australia are through human vectors, avian dispersal as well as some distribution via foxes and other mammals. Human vectors are responsible for dispersal over the longest distances, through nurseries providing stock for the establishment of new groves in diverse areas around the continent [72]. Avian dispersal patterns are generally within several kilometres and may be recognised by seedlings found growing under isolated trees used by birds and along roadsides where perch sites are provided. Introduced bird species, such as blackbird (*Turdus merula*) and starling (*Sturnus vulgaris*) disperse olive seeds in European countries as well as in Australia [73]. In addition, Australian native birds have begun to eat olives as a food source including the emu (*Dromaius novaehollandiae*), magpie (*Gymnorhina tibicen*) and currawong (*Strepera* sp.) [73]. Birds observed feeding and voiding olive seeds in botanic gardens in New South Wales included both introduced and native species [74].

Feral olive stands are a different environment to abandoned olive groves. Bushy habit and smaller fruit size are trends that emerge within populations of feral olives, presumably due to the expression of wild-type characters, as well as the lack of pruning and thinning [44]. Fruit diameter appears to be a crucial factor for avian dispersal [69]. Smaller fruit has a greater chance of being swallowed whole, and these individuals are therefore more likely to be spread over longer distances where they can become the breeding source for new populations [75].

3.1.2. Acacia

The spread of Australian acacias beyond gardens and small plantations into the hills of the Mediterranean basin is an outcome of the dispersal capabilities of these species. A number of agents play a role in the dispersal of the durable acacia seeds (they can survive up to 50 years in the soil). Wind can blow seeds meters from the tree; water may wash seeds even further. Ants are the primary dispersal agents of some Australian acacias (including *A. dealbata, A. mearnsii, A. decurrens*, *A. saligna*, and *A. pycnantha*), while birds are the primary dispersal agents of others (including *A. melanoxylon*, *A. cyclops*, and *A. sophorae*) [76]. Ungulates can also serve as dispersal agents, though research is incomplete on this front [77]. Naturalised *A. dealbata* in the Estérel massif produces large quantities of seeds. Its colonisation of land is facilitated by fires or deep frosts, which destroy trees but stimulate germination and sprouting. The spread of feral *A. dealbata* is naturally limited in south-eastern France by climate (cold tolerance) and geology (limited to the siliceous granitic Estérel and Maures massifs). On the coast, where urbanisation predominates, diffusion is limited to ornamental taxa in gardens and parks.

3.2. Environmental factors limiting dispersal

3.2.1. Olea

In Europe, the wild olive is indifferent to soil pH, although it prefers calcareous soils. Rainfall above 1000 mm limits the olive due to fungal attack by *Verticillium*, in wet soils. Different insects damage, but do not limit the crop or the wild forms. Cold temperatures inhibit olive dispersal as frosts during flower development can adversely affect fruit set and temperatures between −10 and −15 °C can be lethal [79,80].

In Australia, feral olive populations are now widespread in several states in areas with a dry hot summer, predominantly winter rainfall, and sufficient chilling to stimulate flowering in spring [78]. The main infestations occur in areas between 400 and 600 mm annual rainfall [15]. Cold temperatures inhibit olive dispersal as frosts during flower development can adversely affect fruit set and temperatures between −10 and −15 °C can be lethal [79,80]. The spread of *O. europaea* has mainly been in areas with a similar climate to traditional olive growing areas in Europe, in particular in South Australia near Adelaide [81]. However, *O. europaea* subsp. *cuspidata* has become an invasive weed in some subtropical areas in Australia [44].

3.2.2. Acacia

Acacia species introduced to Europe come from Mediterranean, temperate or subtropical climate zones in southeast and southwest Australia, and their spread in introduced areas reflects climate and soil tolerances of their provenance. *A. dealbata*, for example, is native to Tasmania, Victoria, and New South Wales. It tolerates moderate frosts (until about −10 °C) and is thus limited to places in Europe where winters are moderated by proximity to oceans, i.e., the entire Mediterranean coast, the Atlantic coasts of France, Iberia, and the British Isles [6]. *A. saligna*, from coastal south-western Australia, tolerates salty and sandy soils, moderate frosts, and droughts, and has thus found most use in revegetating dune landscapes on Mediterranean islands and in North Africa [64].

4. Hybridization and genetic patterns

4.1. Hybridization of introduced plants

4.1.1. Olea

A native olive (*Olea paniculata*) is found in subtropical regions of Australia, but its potential to cross-hybridize with either of the introduced *O. europaea* taxa is unknown, as no genetic studies have been performed. More important is the potential for introduced olives to hybridize. With the Bayesian method one can estimate the kinship proportion of a tree (cultivar) in one, two or more genetic European classes. A first generation hybrid tree would share 50% of kinship between two cultivars from two different classes, and advanced generations would share less, i.e., 25%, 12.5%, and so on as explained [27]. In Australia the two olive subsp. *cuspidata* and *europaea* may have hybridized leading to individuals acquiring the favourable traits of each subsp., leading to invasive forms.

Microsatellite markers cannot reliably identify hybrid individuals in natural populations although they enable the recognition of given hybrid between two trees of two subsp. Attempts to address this problem by combining the use of microsatellite markers together with an internal transcribe spacer (ITS) marker specific to each subsp. have been made [82]. However, identification of *cuspidata* × *europaea* hybrid trees based on one ribosomal locus is not convincing due to the use of the PCR (amplification of a small piece of DNA) technique. Indeed sublimons (minor variant in an array of repeated sequence) of ITS similar between *cuspidata* and subsp. *europaea* could lead to confusion, as has been shown in sugar beet and other table beet [83]. Moreover, these authors claimed to have identified the origin of *cuspidata* in South Africa where the olive and *cuspidata* may have lead to advanced generation of hybrids between these subsp [84]. However, even though both subsp. have been introduced in Australia, subsp. *cuspidata* × subsp. *europaea* may not cross naturally. This is suggested by experiments provided by P. Villemur (unpublished) in the nursery of Institut National de la Recherche Agronomique in Montpellier which show a shift in blooming by 1 month between the two subspecies. An equivalent situation is found in Morocco where the two subsp. *maroccana* and *europaea* are in sympatry (thrive in the same area), but they did not cross because subsp. *maroccana* blooms 1 month earlier than subsp. *europaea* [85,86].

4.1.2. Acacia

No native acacias exist in Europe, so hybridization only occurs among introduced taxa. Hybridization is well known and common among closely related acacias, such as the bipinnate *A. dealbata, A. decurrens*, and *A. mearnsii* group, both in home ranges in Australia [51] and in areas of introduction [62]. The European garden and flower industry has worked on hybridizing introduced acacias for over a century. The cut flower industry depends most on six different *A. dealbata* × *A. baileyana* hybrids; ornamental plants include a number of other purposely bred hybrids [64]. However, much research remains to be done on Mediterranean acacias. It is unclear, for example, what kinds of interactions exist between feral populations of *A. dealbata*, garden ornamentals, or plantations. Furthermore, the biological affinities of Australian acacias in the region have not been investigated. It is unclear whether feral stands in southern France are restricted only to *A. dealbata* or whether hybrids have also gone feral. To our knowledge, no research exists on hybridization among feral acacias or between feral and cultivated populations (or vice-versa), neither in France nor in Australia.

4.2. Genetic origins of feral trees

Feral olives in Australia can bear similar size fruits to the European olives but have a lower fruit yield compared to subsp. *cuspidata*. Fourteen molecular SSR markers were used to study the diversity of feral Australian trees [27] in comparison to about 850 European cultivated trees. European cultivars could be divided into nine groups [41]. About 60 cultivars have been introduced and feral olives are expected to derive from some of them. However, due to self-incompatibility for most of them we expected that crosses occurred between those cultivars. Consequently, with the set of molecular markers used routinely to identify cultivars we can expect that (the oldest) feral trees should result from crosses between a pair of these introduced European cultivars. With time, further generations have probably mixed again the genome of European cultivars, thus genetic recombination was expected in further generations that correspond to youngest feral trees.

Diversity patterns from Australian feral trees suggest that they were derived from five to six recombination events from European cultivars because they admix with weak probability to each group. Further studies are required to clarify which cultivars were founders and to specify the numbers of tree generations. The present sample did not consider the age of the trees and the cultivars they grow nearby. The older the trees the less recombination events are expected and it will be easier to recognize the sources of cultivars [27].

Genetic variability was also studied between trees of an isolated population on Kangaroo Island, in Southern Australia. The results suggest that feral trees had spread from an original grove by fruit drop, close to the parent trees. Occasional wider dispersal by animals or birds provided source trees from which new populations spread. The data segregated into three clusters that were significantly different from each other. Each cluster contained at least one tree from the original grove as well as other trees from the feral populations, indicating that increasing diversity was created from the original genetic stock [48,87,88]. Australian researchers have started to seek new olive cultivars from feral forms. They identified and vegetatively propagated trees with the best oil quality for field trials [85,89].

Similar research has not been undertaken for acacias in Europe.

5. Conclusion: broad consequences

Humans frequently intentionally move plant species due to their scientific, economic, agricultural, or ornamental value. Occasionally, several taxa within a single genus – like *Acacia* or *Olea* – are transferred, allowing the breaching of natural barriers between taxa in new environments. These case studies, profiled in the present paper, provide a unique opportunity to contrast the operation of cultivar–feral–wild complexes in both native and introduced locations with a view to informing future research and policy debates related to the control of feral and invasive species.

As is already widely known, introduced plants may go feral and become invasive for a number of reasons, yet invasiveness is often unpredictable in character and location. Chief dispersal modes may vary between home range and introduced location; the absence of common predators or parasites of the species in introduced areas can also favour the spread of a plant. In some cases the invasive forms may thrive in soils and climate that mimic their origin, as has been reported for sunflower and prairie sunflower (*Helianthus*) in South America [12]. However, the 'wild' sunflower has become invasive in Southern Europe where the climate and soils are quite different from those of their American home range [11]. If some species thrive more readily than others, it would be interesting to investigate the genes that encode such ability to adapt in diverse environments.

This review has shown that the complexity of genetic relationships between introduced seed stock (whether domesticated and/or wild) and feral plants of a species, as well as relationships between closely related species, can potentially influence the outcomes for plant invasions. This will be of concern to managers involved in the conservation of the genetic state of wild or cultivated populations or the exploitation of the new diversity of the complex as has been done for the feral olive in Australia.

The introduction of exotic plants, whether serendipitous or through organised efforts for scientific, educational, or utilitarian goals, is increasingly regulated. Today's forester, gardener, or cultivator must work methodologically, choose species and provenances carefully, and justify the benefits over the risks of this activity. The current acclimation garden set up in Antibes, southern France is a good example of what can be done in this respect [90]. Introductions are regulated internationally, by treaties such as the Convention on International Trade in Endangered Species (CITES) of 1975, and the Convention on Biological Diversity (CBD) of 1992, as well as nationally, by laws and regulations such as Australia's Quarantine Acts (1908) and its Environmental Protection and Biological Diversity Act (1999).

Phytosanitary precautions are necessary in order to avoid accidental importation of new pests or diseases as occurred in the worldwide spread of plane and elm diseases. The choice and uses of introduced plants and cultivars must take into account the potential risk for invasiveness. Species which can naturalise – a difficult assessment – should be eliminated unless genetic methods are used to prevent spread. For example, wattle flowers would last longer if they were rendered pollen free via transgenic modification or mutagenesis. The plants would have to be vegetatively propagated, but would also preclude pollen allergies. The same could be done for urban plantings of wattles as has been done for plane trees (R. Marie unpublished). Finally, each plant or shipment of seeds must be monitored, from its harvest to its final use, in particular to conserve its genetic identity. Each species is in general introduced with a small number of seeds, in a small population. The most vigourous individuals are chosen. Their descendents, restricted through cloning or sexual reproduction to a small genetic pool, are the ones that will be domesticated. The initial genetic pool is sometimes enriched by subsequent introductions.

A key concern for biologists and environmental managers is to conserve the genetic diversity of local species. It is important to conserve biodiversity through different conservation strategies to maintain pure stocks and to enable controlled hybrids to evaluate their eventual potential for different uses as their potential to escape. However, if species shifts are natural, hybridization between two subspecies from different areas may lead to unexpected hybrid properties. This genetic transgression may deeply modify the ecological behaviour of offspring. Too little regulation and legislation exists to this effect—indeed most invasive plant policy focuses on species and not on sub-species botany. Any such rules must be based on biological features for each species, yet present knowledge on wild species is often limited and lengthy research is necessary to evaluate the risks. They cannot be minimized; zero risk does not exist. In general, however, economic interests dominate over biological considerations in the development of policy. Biologists and environmental managers should explain the risks, including the cascade of events that can be induced by a small initial change, so that decisions can be taken with full knowledge of the risks involved.

It is also worth remembering that climate change will probably cause more modifications to plant population spread and dynamic than species introduction have caused in the European or Australian ecosystems. Climate warming may also change the hierarchy between species and some will probably disappear whereas other will expand. Predictions on what will occur are uncertain due to lack in knowledge on the amplitude of warming and to the behaviour of species faced to warming. Most species could support two or three degrees more without consequence [91].

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