The role of hybridization in facilitating tree invasion

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Abstract. Hybridization events can generate additional genetic diversity upon which natural selection can act and at times enhance invasiveness of the species. Invasive tree species are a growing ecological concern worldwide, and some of these invasions involve hybridization events pre- or post-introduction. There are 20 hybrid invasive tree taxa in 15 genera (11 plant families) discussed here. When reported, abundance of hybrids comprised 10–100 % of an invasion, the remainder being parental taxa. In seven hybrid taxa, researchers identified phenotypes that may make hybrids better invaders. Twelve hybrid tree taxa involved introgression and more hybrids involved all non-native taxa than native × non-native taxa. Three hybrid tree taxa were the result of intentional crosses, and all hybrid taxa involved intentional introduction of either one or more parental taxon or the hybrid itself. The knowledge gaps present in some hybrid tree taxa can weaken our effectiveness in predicting and controlling invasions, as hybrids can add a level of complexity to an invasion by being morphologically cryptic, causing genetic pollution of a native parental taxon, presenting novel genotypes for which there may not be coevolved biological control agents, or evolving adaptive traits through increased genetic variation.

Keywords: Cryptic; hybrid; introgression; invasion; tree.

Introduction

Tree invasions are impacting ecosystems worldwide (Richardson and Rejmánek 2011). The role of hybridization is relatively well-studied in plant invasions (Ellstrand and Schierenbeck 2000), though much less so in invasive tree species. This is partly due to invasive tree species being rarer than other invasive plant forms such as annuals or non-woody perennials and also due to woody plants only recently being recognized as significant invaders (Richardson and Rejmánek 2011). The importance of trees in driving ecosystem architecture and dynamics (Ellison et al. 2005) makes their study essential.

Hybridization can stimulate invasiveness through increasing genetic variation and the creation of novel gene combinations (Stebbins 1959) and can be associated with phenotypes such as increased fecundity and size (Hovick and Whitney 2014) that may enhance invasion. Hybrid events can also help species overcome low genetic diversity resulting from founding events, increasing the odds of successful adaptation (Lee 2002; Schierenbeck and Ellstrand 2009). Hybridization followed by backcrossing of F1s with parental taxa can transfer genes and traits from one taxon to another (introgression), and the resultant progeny may lead to genetic assimilation or genetic pollution with genes and traits.
moving from the native to the non-native species or vice versa, with the former being more common (Currat et al. 2008).

This short review focuses on the following topics: (i) abundance of hybrid trees compared to parental taxa in an invasion; (ii) hybrid phenotypes that may enhance invasions; (iii) the presence of F₁ vs. further hybrid generations and introgression; (iv) the role of native genetic material in invasive tree hybridization; (v) how important intentional hybridization is in contributing to tree invasion and (vi) how often hybrid tree invasions are preceded by intentional vs. accidental introduction. This information is also presented in Table 1 in abbreviated form. In many taxa, not much is known about hybrid tree invasion processes and histories; therefore, a discussion of the research gaps that pertain to understanding and managing hybrid invasive trees is included.

Hybridization is fairly common in plants, with an estimated 11% of species derived from hybrid origins (Ellstrand et al. 1996). The definition of a hybrid used here is the progeny resulting from sexual reproduction between genetically distinct species or lineages that have been reproductively and/or geographically isolated over an evolutionary time scale (as discussed in Rhymer and Simberloff 1996). This can include intra- and interspecific hybrids. Globalization has created unprecedented opportunities for hybridization (Chornesky and Randall 2003), and this special issue is a good opportunity to assess the involvement of hybridization in tree invasions.

The definition of a tree used here is not as precise as in the study by Richardson and Rejmánek (2011; i.e. single trunk, branches held above the ground, apical dominance and >3-m tall), but the species discussed below are typically found in tree form, as opposed to shrub form. This review includes hybrid tree taxa found in Google Scholar searches of combinations of the terms ‘hybrid’, ‘introgression’, ‘invasive’ and ‘tree’.

There is a geographical bias in the study of invasives in general, with Africa (excluding South Africa) and Asia understudied, likely due to financial resource allocation and prioritization in research (Pyšek et al. 2008). We also see the same geographical bias for hybrid tree invasions. Some invasive hybrid tree species are found in more countries and continents than reported here, but this review notes only the invaded continent or country where research was performed. For a more complete listing of invasive tree species distributions, see Rejmánek and Richardson (2013).

I found research data for 20 taxa of hybrid invasive trees in 15 genera in 11 families: Acacia (three hybrid taxa), Leucaena, Paraserianthes, Prosopis (two hybrid taxa) (Fabaceae); Casuarina (Casuarinaceae); Juglans (Juglandaceae); Olea (Oleaceae); Pinus (Pinaceae); Platanus (Platanaceae); Populus, Salix (Salicaceae); Pyrus (Rosaceae); Schinus (Anacardiaceae); Tamarix (three hybrid taxa) (Tamaricaceae); Ulmus (Ulmaceae). Three other hybrid trees appeared in the search; Corymbia torrelliana × C. citriodora (Wallace and Leonhardt 2015), Eucalyptus ovata × E. nitens (Barbour et al. 2003) (both Myrtaceae) and Ulmus pumila × U. minor (Brunet et al. 2013; Ulmaceae), and while invasions by these taxa are an imminent concern, they are not yet documented as invasive, and therefore not included in this review.

How abundant are hybrid trees when part of an invasion?

Not all new genetic combinations are beneficial for adaptation, and not all hybrids have higher fitness than their parental taxa (Seehausen 2004). Admixture can provide advantages for colonizing populations such as heterosis, lower inbreeding depression, novel genotypes, transgressive genotypes that are more extreme in their phenotypes than are parental taxa and increases in population genetic variation (Rius and Darling 2014). Similarly, the abundance of hybrids vs. their parental taxa does not necessarily demonstrate that the hybrid is more or less invasive than its parental taxon (Levine et al. 2003). To more definitively answer the question of which taxon is more invasive requires linking impact on communities and ecosystems and may vary by environmental setting or over time (Pyšek et al. 2012). Studies of invasiveness have been done on hybrid plants (e.g. Vilà and D’antonio 1998; Bleeke and Matthies 2005; Ridley and Ellstrand 2009), but less often on invasive hybrid trees due to rarity of examples, so researchers are usually left with abundance as a proxy for determining invasion success. The measurement of abundance of hybrids in an invasion may be biased by collections that seek out hybrid morphologies, but in some cases hybrids are cryptic, or sampling is random and abundance may reflect that found throughout the invasion.

Casuarina (sheoak, Casuarinaceae) is invasive in Florida, USA, where 34% of the invasives were hybrids between C. glauca and C. equisetifolia as analyzed by Bayesian analysis of amplified fragment length polymorphisms (AFLPs) in STRUCTURE (Pritchard et al. 2000). It was not possible to selectively sample hybrids since they are generally morphologically cryptic, so the abundance of hybrids found by molecular analyses likely reflects that found in the invasion as a whole (Gaskin et al. 2009).

Invasive hybrid Olea (African olive; Oleaceae; Olea europaea ssp. europaea × ssp. cuspidata) in Australia comprised 14% of the invasion in a survey of 11 populations, including one population of 25 individuals that was
Table 1. Information and characteristics for 20 known hybrid tree taxa reported as invasive from any region of the world. The data, including taxonomy, abundance, phenotype, reproductive history, human movement, breeding and use, were gathered from published literature searches. Literature citations for each example can be found in the text of this publication. *Other regions may have been invaded, but region listed is where research on hybrids was performed. Blank cell = information not available.

| Invasive hybrid tree taxon | Intra- or interspecific hybrid | Family | Abundance of hybrids in invasion | Advantageous hybrid phenotype | F2 or introgression present | Native genetic material involved | Intentional hybrids invading | Either parental species introduced intentionally | Invaded region* | Purpose of introduction |
|---------------------------|-------------------------------|--------|---------------------------------|-------------------------------|-----------------------------|-------------------------------|-----------------------------|---------------------------------|----------------|------------------------|
| Acacia pycnantha          | Intra                         | Fabaceae|                                 |                               |                             |                               |                             |                                 | S. Africa, Portugal | tannin production and dune stabilization |
| Acacia cyclops            | Intra                         | Fabaceae|                                 |                               |                             |                               |                             |                                 | S. Africa        | dune stabilization        |
| Acacia saligna            | Intra                         | Fabaceae|                                 |                               |                             |                               |                             |                                 | S. Africa        | dune stabilization        |
| Casuarina glauca × equisetifolia | Inter                   | Casuarinaceae | 34%                           | Yes                            | No                           | No                             | Yes                         | Yes                       | SE USA           | windbreak, shade tree     |
| Juglans × bixbyi (J. cinerea × J. alsinifolia) | Inter                       | Juglandaceae |                              | Yes                            | Yes                          | Yes                            | Yes                         | Yes                       | N. America         | horticulture            |
| Leucaena leucocephala     | Inter                         | Fabaceae|                                 |                               |                             |                               |                             |                                 | Australia         | fodder                 |
|                         | ssp. leucocephala × ssp. glabrata |        |                                 |                               |                             |                               |                             |                                 | Australia         | horticulture, lumber, ornamental |
| Olea europaea ssp. europa × ssp. cuspidata | Intra                     | Oleaceae | 14%                           | Yes                            | No                           | No                             | Yes                         | Yes                       | Australia         | horticulture, lumber, ornamental |
| Paraserianthes lophantha  | Intra                         | Fabaceae| likely                          | No                             | ?                            |                               |                             |                                 | S. Africa and SE Australia | ornamental, forestry |
| Pinus taeda               | Intra                         | Pinaceae| 10–50%                          | None                           | No                           | No                             | Yes                         | Yes                       | S. America       | timber                 |
| Platanus × hispanica (P. occidentalis × P. orientalis) × P. racemosa | Inter                     | Platanaceae |                              | Vigor, disease resistance | Yes                          | Yes                            | No                          | Yes                       | USA              | ornamental              |
| Populus × canadensis      | Inter                         | Fabaceae|                                 |                               | Yes                          | No                             | Yes                         | Yes                       | Australia         | fodder                 |
|                         | (P. deltoides × P. nigra)     |        |                                 |                               |                             |                               |                             |                                 | Europe            | timber                 |

Continued
| Invasive hybrid tree taxon | Intra- or interspecific hybrid | Family          | Abundance of hybrids in invasion | Advantageous hybrid phenotype | F<sub>2</sub> or introgression present | Native genetic material involved | Intentional hybrids invading | Either parental species introduced intentionally | Invaded region* | Purpose of introduction |
|---------------------------|--------------------------------|-----------------|---------------------------------|---------------------------------|--------------------------------------|-------------------------------|--------------------------|-----------------------------------------------|----------------|--------------------------|
| *Prosopis velutina × *P. glandulosa var. glandulosa × *P. pallida |                          | Fabaceae        | wider niche                     |                                 | No                                   | No                            | Yes                      | S. Africa                        | fodder         |                          |
| *Prosopis glandulosa var. Inter toreyana × *P. velutina         |                          | Fabaceae        |                                 | wider niche                     | No                                   | No                            | Yes                      | S. Africa                        | fodder         |                          |
| *Pyrus calleryana       | Intra                        | Rosaceae        | 100 %                           | vigor, expanded niches          | Yes                                  | No                            | No                       | Yes                            | N. America              | ornamental               |
| *Salix × rubens (S. alba × Inter S. fragilis)      |                          | Salicaceae      | Equally abundant as parental taxa? |                                 | No                                   | No                            | Yes                      | Australia                        | shelter, bank stabilization |
| *Schinus terebinthifolius* Intra |                        | Anacardiaceae   | 76 %                            | vigor, biocontrol resistance, new niches | Yes                                  | No                            | No                       | Yes                            | N. America              | ornamental               |
| *Tamarix aphylla × T. ramosissima or T. chinensis* |                        | Tamaricaceae    |                                 |                                 | No                                   | No                            | Yes                      | USA                            | soil stabilization, shade, ornamental |
| *Tamarix ramossimis × Inter T. chinensis* |                        | Tamaricaceae    | 87 %                            | root mass, biocontrol resistance | Yes                                  | No                            | Yes                      | USA                            | soil stabilization, ornamental |
| *Tamarix usneoides × T. ramosissima or T. chinensis* phytoremediation |                        | Tamaricaceae    | 45 %                            |                                 | Yes                                  | Yes                           | No                       | Yes                            | southern Africa          | ornamental               |
| *Ulmus rubra × pumila* Inter |                        | Ulmaceae        | 26 %                            |                                 | Yes                                  | Yes                           | No                       | Yes                            | N. America              | windbreak, shelterbelt, disease resistance |
only hybrids (Besnard et al. 2014), as indicated by a STRUCTURE analysis of simple sequence repeat (SSR) data. Sampling appears to be based on the major invasion hotspots and the original introduction site of cultivated olives (O. europaea ssp. europaea) and did not intentionally seek out hybrids, thus may reflect abundance found in the invasion. *Pinus taeda* (lobolly pine; Pinaceae) was imported from multiple locations in the southeast USA to six locations in southern Brazil as part of a forestry common garden trial. Zenni et al. (2014) found that the intraspecific hybrids accounted for 10–50% of the invading trees when measured by STRUCTURE analysis of single-nucleotide polymorphisms. Sampling was haphazard, and the hybrids were morphologically cryptic, so it is likely that the abundance of hybrids found in the analysis reflects that found in the invasion as a whole.

*Prosopis* (mesquite; Fabaceae), is an introduced hybrid swarm in Australia made from three species (*P. velutina* × *P. glandulosa* var. *glandulosa* × *P. pallida*), and the whole Australian invasion consists of the hybrid (van Klinken et al. 2006). In the case of *Pyrus calleryana* (Callery pear; Rosaceae) invading the USA, where two genetically distinct cultivars from China have been brought together, the parental taxa are self-incompatible, so the intraspecific hybrids make up 100% of the invasion, according to STRUCTURE analysis using SSRs (Culley and Hardiman 2009). In this case, it is clear that hybrids are more invasive than parental taxa.

*Salix* × *rubens* (Salicaceae), a hybrid of European *S. alba* and *S. fragilis* found in Australia, is reportedly as abundant as its invasive parental taxa (Adair et al. 2006) though the source of this conclusion is unclear (and not the focus of that article).

For invasive *Schinus terebinthifolius* (Brazilian pepper-tree; Anacardiaceae) in Florida, USA, intraspecific hybrids comprised 76% of the invasion as measured by SSRs in STRUCTURE analysis (Williams et al. 2005). As the morphological characters for distinguishing varieties are broadly overlapping, sampling appears to have been done without prior knowledge of hybrid status, and reported abundance likely represents that found in the invasion.

*Tamarix* spp. (tamarisk; Tamaricaceae) have formed hybrid invasions in both North America and southern Africa. In the USA, AFLP analysis using NewHybrids (Anderson and Thompson 2002), determined that hybrids of *T. ramosissima* × *T. chinensis* from Asia accounted for up to 87% of the invasion (Gaskin and Kazmer 2009). The hybrids are virtually indistinguishable between these sister species, so the sampling across the western USA likely reflects what is found throughout the invasion. Another *Tamarix* hybrid between both *T. ramosissima* or *T. chinensis* × *T. aphylla* (athel tamarisk) is found in western USA, and samples were selected for their obvious morphological intermediacy between *T. ramosissima*/*T. chinensis* and the distantly related *T. aphylla* at three locations (Gaskin and Shafroth 2005). This suggests that the hybrid is highly limited in abundance, as the morphology had not been noted in other locations. The intermediate morphology was correlated with the heterogeneous combinations of species specific nuclear DNA, verifying hybrid status. In southern Africa, Mayonde et al. (2015) found hybrids of *T. ramosissima* × *T. usneoides* (the latter being native) using nuclear and chloroplast DNA sequencing. The hybrid comprised 45% of the sampled plants. Samples were sought by morphology, so hybrid abundance may not reflect that of the invasion as a whole.

For invasive *Ulmus* (elm; Ulmaceae; *U. pumila* × *U. rubra*) in the USA, Zalapa et al. (2010) used species-specific alleles of SSRs and a STRUCTURE analysis and found that 26% of the naturalized *U. pumila* plants were hybrids. Some plants may have been selected for morphological intermediacy, so this may be an overestimate of hybrid abundance throughout the invasion.

**Are there hybrid phenotypes that enhance invasion?**

Certainly not all hybrid progeny are better at invading than their non-native parents (Rius and Darling 2014), but some studies have noted phenotypes that may enhance invasive ability, or alter levels of insect and pathogen tolerance or resistance. For the *Juglans* × *bixbyi* system (butternut; Juglandaceae; a hybrid of native *J. cinerea* and Asian *J. ailantifolia*), seeds of the invasive hybrid trees in the USA are collected for food, moved and planted in new locations by the public. The hybrid taxon is more vigorous and higher yielding than the USA native species (Farlee et al. 2010) though this is not described quantitatively and has better resistance to canker (Orchard et al. 1982). They are also a source of genetic pollution to the native butternut *J. cinerea*, which is becoming threatened and rare due to attack by the fungus *Sirococcus clavigignenti-juglandacearum* (Woeste et al. 2009).

Zenni et al. (2014) investigated factors of range expansion of the parental and intraspecific hybrid genotypes of *Pinus taeda* in Brazil. An interaction between genetic provenance from the USA and climate in Brazil predicts the invasive performance of particular genotypes. Hybridization was not found to be a major driver of invasion (hybrids did not spread further than parental genotypes), and parental genotypes were able to exploit niches that are very different from those in their native range.
Platanus (sycamore; Platanaceae) hybrids in the USA (P. hispanica [a hybrid of P. occidentalis (eastern USA) × P. orientalis (Eurasia)] × P. racemose [western USA]) are claimed to exhibit hybrid vigor and do have higher resistance to root diseases compared to both the native and non-native parents (Johnson et al. 2016). Prosopis hybrids in Australia are more fire tolerant than one of its parental taxa; P. pallida (van Klinken et al. 2006), and hybrids may exist in a wider array of niches than parental taxa in South Africa (Poynton 1990).

In the case of Pyrus calleryana, the hybrids, as mentioned above, are invasive and the parental taxa are not due to self-incompatibility. The parental taxa are only spread by human-mediated clonal reproduction, while the hybrids spread by seed, demonstrating a huge enhancement of invasive ability through hybridization. In a further study, early generation hybrids had greater belowground biomass than parental taxa, which may indicate hybrid vigor, while the parental taxa may be better adapted to cultivated conditions (Hardiman and Culley 2010).

For Schinus terebinthifolius in the USA, invasive hybrids are the combination of two allopatric native lineages, and one thrips biological control agent showed no survival to the adult stage on the invasive hybrids, but was reared successfully on the Brazilian lineages (Manrique et al. 2008), suggesting that the hybrid may better resist this biological control agent. In the same system, Geiger et al. (2011) demonstrated hybrid vigor, with 45 % more seedling establishment for the hybrids compared to parental genotypes. Also, new niches are occupied by Schinus hybrids compared to the more limited niches of parental lineages (Mukherjee et al. 2012), and an ecological niche model predicted that the hybrid could eventually invade a large portion of the southeastern USA, while the parental taxa would be restricted to Florida.

For invasive Tamarix in the USA, higher levels of introgression towards T. ramosissima resulted in higher investments in root mass and higher tolerance to defoliation by the biological control agent Diorhabda carinulata (Williams et al. 2014), suggesting an advantage for the hybrid invasive over the parent T. chinensis.

**F1 vs. further hybrid generations and introgression**

Further sexual reproduction between F1s (first-generation hybrids) and/or backcrossing with parental types can lead to an increased number of hybrid and introgressed genotypes for natural selection to act upon, therefore determining the presence of F1 and introgressed individuals can give useful information about potential adaptation and further invasion of a hybrid. Twelve hybrid tree invasions are noted to have F2s (F1 × F2) or introgressed individuals, including intraspecific hybrids of Acacia saligna in South Africa (Thompson et al. 2012), Casuarina (Gaskin et al. 2009), Juglans (Hoban et al. 2009), Olea (introgression; Besnard and El Bakkali 2014), Platanus (introgression; Johnson et al. 2016), Prosopis (hybrid swarm; van Klinken et al. 2006), Pyrus (introgression; Culley and Hardiman 2009), Schinus (introgression; Williams et al. 2005), Tamarix ramosissima × T. chinensis (introgression; Gaskin and Kazmer 2009), Tamarix usneoides × T. ramosissima or × T. chinensis (Mayonde et al. 2016) and Ulmus (F1 and backcrosses; Zalapa et al. 2010). Introgression was typically determined through Bayesian analysis of SSRs or AFLPs. The studies of other invasive tree hybrid taxa did not state whether or not F2 or backcrosses existed, but that was not the focus of their research.

**The role of native genetic material in invasive tree hybridization**

Sexual reproduction between native and non-native species creates novel hybrids of species that have been reproductively isolated from each other for perhaps millions of years. Novel hybrids can also come about when two or more previously disjunct non-natives are placed in close enough proximity for sexual reproduction. Novel hybrid taxa may be required to identify non-natives before making control decisions. Additionally, novel hybrids may share zero evolutionary history with host-specific herbivores used in biological control, so testing of agents against the novel hybrid (e.g. Williams et al. 2014) becomes a priority. The following hybrid tree species involved native genetic material: Juglans (Hoban et al. 2009), Platanus (Johnson et al. 2016), Populus (Vanden-Broeck et al. 2012), Tamarix in southern Africa (Mayonde et al. 2015) and Ulmus (Zalapa et al. 2010).

Novel hybrid invasives that involved only non-native species include Acacia pycnantha, A. saligna and A. cyclops (intraspecific hybrids; Le Roux et al. 2011; Thompson et al. 2012; Ndlovu et al. 2013), Casuarina (interspecific hybrid; Gaskin et al. 2009), Leucaena (white leadtree; Fabaceae; an intraspecific hybrid with origins in North and...
Central America and now invading Australia; Raghu et al. 2005), *Olea* (interspecific hybrid; Besnard and El Bakkali 2014), *Paraserianthes* (Cape Leeuwin wattle; Fabaceae; an intraspecific hybrid of geographically structured Australian native sources now invading South Africa; Thompson et al. 2016), *Pinus taeda* (intraspecific hybrid; Zenni et al. 2014), *Prosopis* (interspecific hybrid; Van Klinken et al. 2006), *Pyrus* (intraspecific hybrid; Hardiman and Culley 2010), *Salix* (interspecific hybrid; Greenwood et al. 2004), *Schinus* (intraspecific hybrid; Williams et al. 2005) and *Tamarix* (interspecific hybrids; Gaskin and Schaal 2002, Gaskin and Shafroth 2005).

How important is intentional hybridization in contributing to invasion?

Tree breeding programs and importation are common and intentional introductions of trees lead to invasion more often than do accidental introductions (Richardson and Rejmánek 2011). Purposeful breeding through hybridization can hasten adaptation for invasion (e.g. Laikre et al. 2010). For hybrid trees, we see few examples of intentional hybridization preceding invasion, although there is a lack of information in some systems. Only four taxa in this review had intentional hybridization preceding invasion. *Casuarina* hybrids have been created intentionally (Ho et al. 2002, Zhong et al. 2010; Ho and Lee 2011) in Taiwan and China, without reports or concerns of invasion, while there are no reports of intentional hybridization in the US invasion (Woodall and Geary 1985). *Juglans* hybrids were created intentionally and a *Prosopis* invasion in Australia (*P. velutina* × *P. glandulosa* var. *glandulosa* × *P. pallida*) was formed from intentional hybrids (van Klinken et al. 2006). In the *Tamarix ramosissima* × *T. chinensis* invasion, intentional hybridization for horticulture likely occurred in the 1800s on the east coast of the USA (Brotherson and Von Winkel 1986), but the species rarely persist there (Gaskin in press). The main invasion is in the western North America, and a DNA study of tree age classes in Utah, USA, showed that even trees that sprouted back in the 1930s were all hybrids (Gaskin et al. 2012) though the invasion was only first reported in 1925 (Christensen 1962).

Were any parents of the hybrids intentionally introduced?

All hybrid invasive tree species that are discussed in this article have had intentional introductions in their history. The specific reasons for introduction of one or both parental taxa, or the direct introduction of the hybrid, are as follows (or see abbreviated list in Table 1): *Acacia pycantha*, for tannin production and dune stabilization (Ndlovu et al. 2013), and *A. cyclops* and *A. saligna* for dune stabilization (Le Roux et al. 2011). *Casuarina* parental species were brought to the USA as a windbreak and shade tree (Wheeler et al. 2011). *Juglans ailantifolia* was imported into the USA for horticulture uses (Zhao and Woeste 2011). *Leucaena* was introduced to Australia for forage (Raghu et al. 2005). *Olea* parental species were introduced for cultivation, lumber and as ornamentals (Besnard et al. 2014). *Paraserianthes* parental taxa were imported to South Africa for ornamental and forestry uses (Le Roux et al. 2011). *Pinus taeda* was imported to Brazil for timber production (Zenni et al. 2014). *Platanus × hispanica* was imported to the USA as an ornamental (Johnson et al. 2016). *Populus* hybrids were introduced to Europe for timber (Vanden-Broeck et al. 2012). *Prosopis* hybrids were introduced to South Africa as fodder (Poynton 1990). *Pyrus calleryana* was brought to the USA from Asia as an ornamental (Culley and Hardiman 2009). *Salix* was brought from Europe and Asia to be planted along rivers and streams to stabilize banks and provide shelter for livestock (Greenwood et al. 2004). Both *Schinus terebinthifolius* lineages were brought from South America to the USA as ornamentals (Williams et al. 2005). *Tamarix* species were brought to the USA as ornamentals (Brotherson and Field 1987), but later spread through the western USA due to their use for shade and for erosion control (Baum 1967). *T. ramosissima* was introduced to South Africa as an ornamental, but now, unintentional hybrids between it and the native *T. usneoides* are being used in phytoremediation on mining sites (Mayonde et al. 2015). *Ulmus pumila* was introduced to the USA as a windbreak and shelterbelt and as a source of disease resistance genes in elm breeding programs (Webb 1948; Smalley and Guries 2000).

Discussion

Overall, invasive hybrid trees represented 10–100% of total individuals sampled in the examples discussed above. Again, this number may be biased by collection method, and even high abundance does not necessarily correlate with high invasive impact. Also, trees can be slow to reach maturity, and a young hybrid invasion (i.e. consisting of F1s) may not reflect the ecological damage that will occur if the trees start to produce further hybrid generations. To better understand the impact that hybrid trees have on the invasion, we at least need to know their abundance as an initial proxy for invasiveness, while realizing that abundance can be an effect of initial hybrid propagule pressure and not necessarily correlated to invasiveness. Random sampling of trees in invasions is needed to assess abundance, as opposed to selectively sampling hybrid morphologies. Studies that combine
hybrid demographic with analysis of evolutionary and ecological drivers of invasion (e.g. Zenni et al. 2014) will be the key to determining the importance of hybridization in each tree invasion.

We rarely know the phenotypes of hybrids that make them more or less invasive than parental taxa. This limits control efficacy as we do not know what age, phenology, or part of the plant to control when our limited resources or management options do not permit killing all individuals of the invasion. We can perform more effective control if we know if hybrid tree invasiveness is enhanced by phenotypes such as cold tolerance, high seed output, shifted phenology, disease resistance, etc. To robustly test for increased invasiveness, common garden experiments of fitness, defensive chemistry, adaptive ecophysiological traits, etc., which are performed on many invasive plants (e.g. Bossdorf et al. 2005; Cano et al. 2008; DeWalt et al. 2004) can be applied to invasive hybrid trees, though the long period of maturation for many trees may be a hindrance to the research. Hybrid vigor phenotypes may break down after further generations of hybrid reproduction or backcrossing (Edmands 1999), so there may be variation in invasive ability of hybrids by age class. Not all hybrids in an invasion are likely to have the advantageous phenotype in all environments, so suggesting that some of these hybrids are better invaders than parental taxa may be unwarranted (see Pyšek et al. 2012).

Introgression in hybrid tree invasion is an important knowledge gap that could help prediction of further invasion, increases in genetic diversity and adaptation, genetic assimilation and genetic pollution. Introgression, though typically morphologically cryptic, is easily detected with multi-loci molecular markers that vary between parental taxa (see research examples in ‘F1 vs. further hybrid generations and introgression’ section) and should be explored when suspected in an invasion.

The presence or abundance of novel hybrids can have strong effects on management, especially biological control. Discovery of novel hybrids is relatively straightforward with careful morphological analysis or molecular analysis if parental species are allopatric. If parental native ranges overlap, more extensive native sampling will be needed to see whether the hybrid is only found in the invasion (e.g. Gaskin et al. 2009).

Though examples of intentionally bred hybrid trees becoming invasive are few, their existence suggests that we need effective risk analysis for breeding and importing hybrid plants, as adaptations for cultural use may also be adaptations for high fitness and invasion success. The themes of introduction are common: fodder, timber, ornamental use and landscape stabilization and show a pattern that further illustrates the need for careful introduction of non-native trees. The fact that none of the hybrid invasive tree taxa discussed here are the result of accidental introduction of parental or hybrid taxa shows that regulation of tree imports could stop most future hybrid tree invasions.

Conclusion

What we do not know about hybrid invasive trees limits our ability to control the invasion as a whole. Hybrid abundance can vary widely and in some cases has not been evaluated. That can hinder our ability to prioritize control of parental vs. hybrid taxa if such a distinction is desired. Knowledge of F1 vs. further hybrid generations is lacking in many cases, making it impossible to assess potential adaptation of hybrids via genetic assimilation of native traits and conversely genetic pollution of native parental taxa. Five out of 20 invasions included a native species as a parental taxon of the hybrid and these cases not only create novel hybrids but also lead to management and conservation issues such as genetic pollution and potential lack of co-evolved and thus highly host-specific biological control agents. Unintentional hybridization occurred in 10 out of 20 cases, which illuminates the risk of intentionally introducing exotic congeners without an evidence-based white list program. In many cases a clearer understanding of hybrid invasion processes and phenotypes, important knowledge in all invasions, will be required before we can develop effective management strategies.

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Contributions by the Authors

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None declared.
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