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# Tree invasions: a comparative test of the dominant hypotheses and functional traits

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**Abstract** Trees act as ecosystem engineers and invasions by exotic tree species profoundly impact recipient communities. Recently, research on invasive trees has dramatically increased, enabling the assessment of general trends in tree invasion. Analysing 90 studies dealing with 45 invasive tree species, we conducted a quantitative review and a meta-analysis to estimate the relevance of eight leading hypotheses for explaining tree invasions. We also tested whether species functional traits (growth rate, density/cover, germination, biomass and survival) equally promote tree invasiveness. Overall, our results suggest that several hypotheses, linked to invasibility or invasiveness, are pertinent to explain tree invasions. Furthermore, more than one hypothesis has been supported for a given species, which indicates that multiple factors lead to the success of invasive tree species. In addition, growth rate appears to be the most efficient predictor of invasiveness for invasive trees and could thus be used as a means to identify potential alien tree invasions. We conclude that further investigations are needed to test the consistency of some hypotheses across a broader pool of invasive tree species, whilst experimental studies with the same tree species across a larger range of sites would help to reveal the full suite of factors that affect tree invasions.

**Keywords** Tree invasion · Systematic review · Meta-analysis · Invasiveness · Invasibility · Functional traits

## Introduction

Over the last few decades, biological invasions have become a pressing topic in ecology and evolution, particularly in population biology, community ecology, restoration, and conservation biology (Sakai et al. 2001; Callaway and Maron 2006). Their negative impacts on recipient communities include alteration of successional dynamics over time, reduction of diversity and relative abundance of native species, disruption of important ecosystem functions as well as strong economical costs induced to limit their proliferation (Inderjit 2005). Virtually no places are immune from changes related to invasions (Mack et al. 2000).

As described by Wardle (2002), community and ecosystem processes are controlled by keystone species. In forests, trees play the role of ecosystem engineers and regulate ecosystem functions (Reich et al. 2001; Crooks 2002; Belote and Jones 2009). Consequently, ecosystem invasions by woody species can lead to serious changes in community functions, altering primary production, biomass distribution,

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litterfall and decomposition rates, energy balance or carbon storage (Richardson and Higgins 1998; Jackson et al. 2002; Yelenik et al. 2004). For instance, Australian *Acacia* spp. account for the most significant declines in native species richness in the Fynbos Biome of South Africa (see Richardson and van Wilgen 2004 for review; Gaertner et al. 2009), whilst *Tamarix* spp. prevent natural flood regimes and deepen local water tables in the Southwestern USA (Randall 1993, 1996).

Growing concern about tree invasions in recent decades has promoted their adoption as a suitable model to understand invasion processes in general (Richardson and Bond 1991; Krivanek and Pysek 2006; Richardson 2006; Pysek et al. 2009). While a recent review presents evidence for 357 tree species being invasive in at least one region of the world (Richardson and Rejmanek, in press), studies have predominantly featured conifer tree invasions in the Southern Hemisphere (Richardson et al. 1994; Higgins et al. 1996; Richardson 1998; Simberloff et al. 2010) and broadleaved deciduous tree invasions in the Northern Hemisphere (Keay et al. 2000; Rogers and Siemann 2002; Chabrerie et al. 2008; Cincotta et al. 2009). In addition, invasions by tree species have been investigated through the use of multiple functional traits such as survival and herbivory resistance, germination, growth, biomass accumulation, density and abundance (Siemann and Rogers 2001; Chaneton et al. 2004). Consequently, the capacity now exists to quantitatively assess the literature on invasive trees and to determine general trends such as which functional traits are determinants of tree invasiveness, which community-level attributes promote tree invasions, and which research gaps should be addressed in subsequent studies (Rejmánek 1996; Rejmánek and Richardson 1996).

Several hypotheses have been postulated to explain the success of introduced plants (Hierro et al. 2005). They focus either on community, habitat or ecosystem-level properties that relate to the susceptibility to invasion (invasibility, Williamson 1996; Lonsdale 1999) or on species life-history traits that promote successful colonization of exotics (invasiveness, Williamson and Fitter 1996). Specifically, invasibility is defined as the features of the environment or components of a community that determine its vulnerability to invasion, while invasiveness refers to the features of an alien organism, such as its life-history traits and mode of reproduction, that define its capacity to invade (Sakai et al. 2001; Erfmeier and Bruelheide 2010; Richardson et al. 2011). A species may become invasive (1) if its entry in the community is facilitated by native species (theory of facilitation; Bruno et al. 2003), (2) if natural or anthropogenic disturbances affect the community (disturbance hypothesis; Mack et al. 2000) or (3) when fluctuating resources through time and space (theory of fluctuating resource availability; Davis et al. 2000) or vacant niches (empty niche hypothesis; Mack 1996; Levine and D'Antonio 1999) are available. On the other hand, functional traits have been extensively studied as a means to potentially predict invasiveness (Sakai et al. 2001). For instance, some exotic grass and tree species have been found to produce high numbers of seeds (propagule pressure hypothesis; Williamson and Fitter 1996; Lonsdale 1999) or to use allelopathic compounds towards native species (novel weapons hypothesis; Callaway and Aschehoug 2000). Escaping from natural enemies, plant species can also exhibit a rapid increase in distribution and abundance (enemy release hypothesis; Keane and Crawley 2002) whilst evolutionary changes may occur as plants reallocate their resources previously reserved for defense to growth and reproduction (evolution of increased competitive ability hypothesis; Blossey and Notzold 1995). Initially proposed for weedy invasions into grasslands (Maron and Vila 2001), these mechanisms may also apply to tree invasions.

Quantitative reviews have the capacity to provide a means of assessing progress to date in studying invasions and highlighting gaps in research. Such an approach applied to invasive trees would offer both a broad picture of the importance of tree invasions in forest systems and an assessment of the effectiveness of the set of studies available to date. Here, we incorporated a formal systematic review together with meta-analytical statistics to assess the following questions in the specific context of invasive tree species: (1) Do hypotheses linked to invasiveness or invasibility equally contribute to explaining tree invasions? (2) Is the success of a given invasive tree species explained by one or more hypotheses? (3) Which functional traits are the best determinants of tree invasiveness?

We used the standardized terminology recommended by Richardson et al. (2000) to define species' invasion status. In this study, an 'invasive' species is a naturalized alien (synonyms: exotic, non-native) plant that produces reproductive offspring in very large numbers at considerable distances from parents plants, and thus have the potential to spread over a considerable area (Richardson et al. 2000; Pysek et al. 2004). Similarly, 'invasion success' refers here to species that have been successful in both establishing and spreading in areas beyond their native range, which is an opportunity limited to a small fraction of introduced taxa (Richardson et al. 2000; Williamson 2006; Blackburn and Jeschke 2009). We included in this study tree species only, defined as in Richardson and Rejmanek (in press). For inclusion in this study, articles had to focus on invasive tree species and effectively tested at least one of the eight dominant invasion hypotheses.

## Materials and methods

### Systematic review

This systematic review focused on the eight most common hypotheses associated with invasive species in general. Four of these are linked to the invasiveness concept, the enemy release (ER) hypothesis (Keane and Crawley 2002), the evolution of increased competitive ability (EICA) hypothesis (Blossey and Notzold 1995), the novel weapons (NW) hypothesis (Callaway and Aschehoug 2000) and the propagule pressure (PP) hypothesis (Williamson and Fitter 1996; Lonsdale 1999), while four are encapsulated in the invasibility concept, the empty niche (EN) hypothesis (Levine and D'Antonio 1999), the theory of fluctuation of resource availability (FRA) (Davis et al. 2000), the theory of facilitation (Bruno et al. 2003) and the disturbance hypothesis (Mack et al. 2000). Using the Web of Science (ISI) electronic bibliographic database, an extensive literature survey was conducted through a set of key words including 'enemy release', 'competitive ability', 'allelopathy', 'propagule pressure', 'niche hypothesis', 'fluctuating resource', 'facilitation', and 'disturbance hypothesis'. Observational, experimental and modelling studies were included provided they focused on factors associated with promoting invasions. However, modelling studies that mapped plant population distributions in their invasive ranges were excluded from the set of studies used in the formal meta-analyses since they did not explicitly test hypotheses. Publications were then classified as follows: how many (a) cited each hypothesis, (b) tested it in practical terms on plant invasions, and (c) tested it on invasive tree species. All the articles that were listed on the Science Citation Index as of early November 2010 and that met the inclusion criteria were included. A vote-counting method was used to assess the success of testing each hypothesis on invasive trees (Gates 2002).

### Meta-analyses

Using the pool of experimental and observational publications from the systematic review which focused on invasive trees, we performed two meta-analyses: one on the hypotheses tested and one on the main functional traits measured in tree invasion ecology and linked to invasiveness. Because it takes into account the effect of small sample sizes (Hedges and Olkin 1985; Rosenberg et al. 2000), Hedges' unbiased standardized mean difference (Hedges' $d$) was used as the metric of effect size for both meta-analyses. Hence, studies were included only if a measure of the sample size and the error term of the mean values were available for both control and treatment groups. These values were obtained either from text, tables, or graphs. Data published in graph form were extracted using TechDig 2.0 software (Jones 1998). Mean, sample size and error term data which were not provided in the publications nor obtained by contacting the authors were excluded from the analyses.

In the first meta-analysis, performed to assess whether the leading hypotheses for plant invasion are all relevant to explain the success of invasive trees, control and treatment groups used for effect size calculations in a publication were determined to be in accordance with the hypothesis tested (see "Appendix 1"). Accordingly, we changed the sign of the effect sizes for the studies related to the novel weapons hypothesis because negative values of the effect sizes actually indicated an inhibitory effect of the invasive species on the native neighbours. Moreover, in order to avoid pseudo-replication, effect sizes in a publication were pooled per species and per hypothesis tested, and we thus used the pooled mean effect size and the mean variance (Leimu et al. 2006; van Kleunen et al. 2010). Therefore, the final data set included 63 studies reported in 58 publications that encompassed 26 invasive tree species (Table 1).

**Table 1** List of articles that effectively tested one of the eight dominant invasion hypotheses on invasive tree species

| References | Invasive tree species | Study location | Hypothesis[a] | Trait[b] |
|---|---|---|---|---|
| Adams et al. (2009)[‡,§] | *Acer platanoides* | North America and Europe | ER | S |
| Alston and Richardson (2006) | *Acacia* spp., *Eriobotrya japonica*, *Homolanthus populifolius*, *Paraserianthes lophantha*, *Pinus* spp., *Pittosporum undulatum*, *Populus × canescens*, *Quercus robur*, *Solanum mauritianum* | South Africa | D | – |
| Barton et al. (2004) | *Acer platanoides*, *Rhamnus cathartica* | USA | PP | – |
| Battaglia et al. (2009) | *Sapium sebiferum* | USA | F | – |
| Bellingham et al. (2005)[‡,§] | *Pittosporum undulatum* | Jamaica | EN | DC |
| Belote et al. (2008) | *Ailanthus altissima* | USA | EN | – |
| Carvalho et al. (2010)[‡,§] | *Acacia longifolia* | Portugal | D | B |
| Chabrerie et al. (2008) | *Prunus serotina* | France | D | – |
| Chaneton et al. (2004)[‡,§] | *Gleditsia triacanthos* | Argentina | D | B, Ge, S |
| Cincotta et al. (2009)[‡,§] | *Acer platanoides* | USA | ER | B, S |
| Conway et al. (2002) | *Sapium sebiferum* | USA | NW | – |
| Dezotti et al. (2009) | *Pinus ponderosa*, *Pinus radiata* | Argentina | PP | – |
| Donnelly and Walters (2008)[‡] | *Schinus terebinthifolius* | USA | PP | DC, Ge, S |
| Donnelly et al. (2008)[‡] | *Schinus terebinthifolius* | USA | NW | B, Gr |
| Franks et al. (2008a)[‡,§] | *Melaleuca quinquenervia* | USA | EICA | B, Gr |
| Franks et al. (2008b) | *Melaleuca quinquenervia* | USA | EICA | – |
| Green et al. (2004)[‡] | *Adenanthera pavonia* | Australia | ER | B, Gr |
| Gurevitch et al. (2008) | *Acer platanoides*, *Prunus serotina* | USA | FRA | – |
| Heimpel et al. (2010) | *Rhamnus cathartica* | USA | F | – |
| Higgins and Richardson (1998) | *Pinus radiata*, *Pinus strobus* | South Africa | D | – |
| Higgins et al. (1996) | *Pinus* spp. | South Africa | PP | – |
| Howard et al. (2004) | *Ailanthus altissima*, *Robinia pseudo-acacia* | USA | EN | – |
| Huang et al. (2010)[‡,§] | *Sapium sebiferum* | USA | EICA | – |
| Iponga et al. (2009a)[‡] | *Schinus molle* | South Africa | PP | – |
| Iponga et al. (2009b)[‡] | *Schinus molle* | South Africa | F and ER | – |
| Iponga et al. (2010)[‡] | *Schinus molle* | South Africa | F | – |
| Kaproth and McGraw (2008)[‡] | *Ailanthus altissima* | USA | PP | – |
| Keay et al. (2000) | *Sapium sebiferum* | USA | NW | – |
| Knapp et al. (2008)[‡,§] | *Acer platanoides*, | USA | ER | Gr, S |
| Knight and Reich (2005) | *Rhamnus cathartica* | USA | EN | – |
| Knight et al. (2008) | *Prunus serotina* | Poland | EN | – |

**Table 1** continued

| References | Invasive tree species | Study location | Hypothesis[a] | Trait[b] |
|---|---|---|---|---|
| Krivanek et al. (2006) | *Acer negundo*, *Ailanthus altissima*, *Padus serotina*, *Pinus strobus*, *Quercus rubra*, *Robinia pseudo-acacia* | Czech Republic | PP | – |
| Kuppinger et al. (2010) | *Paulownia tomentosa* | USA | D | – |
| Lankau et al. (2004)[‡,§] | *Sapium sebiferum* | USA | ER | B, S |
| Leger et al. (2007)[§] | *Acer platanoides* | USA | FRA | B |
| Lesica and DeLuca (2004)[‡] | *Tamarix ramosissima* | USA | NW | Gr |
| Liu et al. (2007)[‡,§] | *Eugenia uniflora* | USA | ER | Ge, S |
| Lockhart et al. (1999)[‡] | *Melaleuca quinquenervia* | USA | FRA | – |
| Lorenzo et al. (2008)[‡] | *Acacia dealbata* | Spain | NW | – |
| Lorenzo et al. (2010a)[‡,§] | *Acacia dealbata* | Spain | NW | Ge, Gr |
| Lorenzo et al. (2010b) | *Acacia dealbata* | Spain | NW | – |
| Martin and Canham (2010)[‡,§] | *Acer platanoides*, *Ailanthus altissima* | USA | PP | DC |
| Martin and Marks (2006)[‡] | *Acer platanoides* | USA | FRA | – |
| Mazia et al. (2001)[‡] | *Gleditsia triancathos*, *Prosopis caldenia* | Argentina | D | – |
| Mazia et al. (2010)[‡,§] | *Gleditsia triacanthos* | Argentina | D | S |
| McCay and McCay (2009)[‡,§] | *Rhamnus cathartica* | USA | PP | DC, S |
| Milton et al. (2007) | *Prosopis* sp., *Schinus molle* | South Africa | PP | – |
| Morgan and Overholt (2005)[‡] | *Schinus terebinthifolius* | USA | NW | – |
| Morrison and Mauck (2007)[‡,§] | *Acer platanoides* | USA | ER | B, Gr, S |
| Nasir et al. (2005)[‡] | *Robinia pseudo-acacia* | Japon | NW | – |
| Nijjer et al. (2007)[‡,§] | *Sapium sebiferum* | USA | F | B, Gr, S |
| Nunez et al. (2008) | *Pinus ponderosa*, *Pseudotsuga menziesii* | Argentina | F | – |
| Ohlemüller et al. (2006) | – | New Zealand | EN | – |
| Peperkorn et al. (2005)[‡,§] | *Acacia longifolia* | Germany | FRA | B, Gr |
| Reinhart and Callaway (2004)[‡,§] | *Acer negundo*, *Acer platanoides* | USA and France | ER | B, Gr |
| Reinhart et al. (2003)[‡,§] | *Prunus serotina* | USA and The Netherlands | ER | B |
| Reinhart et al. (2005)[‡,§] | *Acer platanoides* | USA | F | B, Gr |
| Reinhart et al. (2006)[‡] | *Acer platanoides* | USA | F | – |
| Reinhart et al. (2010)[‡,§] | *Prunus serotina* | Belgium | ER | B, S |
| Relva et al. (2010)[‡,§] | *Pseudotsuga menziesii* | Argentina | F | DC, Gr |
| Reynolds and Cooper (2010)[§] | *Elaeagnus angustifolia* | USA | F | Gr |
| Richardson and Bond (1991) | *Pinus* spp. | South Africa | D | – |
| Richardson et al. (1994) | *Pinu* spp. | South Africa | D | – |

**Table 1** continued

| References | Invasive tree species | Study location | Hypothesis[a] | Trait[b] |
|---|---|---|---|---|
| Rogers and Siemann (2002)[‡,§] | *Sapium sebiferum* | USA | ER | Gr |
| Rogers and Siemann (2003)[‡] | *Sapium sebiferum* | USA | ER | – |
| Rogers and Siemann (2004)[‡,§] | *Sapium sebiferum* | USA | EICA | B, Gr |
| Rogers and Siemann (2005)[‡,§] | *Sapium sebiferum* | USA | EICA | B, Gr |
| Rouget and Richardson (2003) | *Acacia saligna*, *Acacia cyclops*, *Pinus pinaster* | South Africa | PP | – |
| Rouget et al. (2001) | *Pinus canariensis*, *Pinus halepensis*, *Pinus pinaster*, *Pinus radiata* | South Africa | D | – |
| Saccone et al. (2010) | *Acer negundo* | France | F | – |
| Schumacher et al. (2008)[‡,§] | *Alstonia macrophylla*, *Cinnamomum verum*, *Psidium cattleianum*, *Syzygium jambos*, *Tabebuia pallida* | Seychelles | FRA | B, Gr |
| Schumacher et al. (2009)[‡,§] | *Alstonia macrophylla*, *Cinnamomum verum*, *Psidium cattleianum*, *Sandoricum koetjape*, *Syzygium jambos*, *Tabebuia pallida* | Seychelles | FRA | B, Gr |
| Siemann and Rogers (2001)[‡,§] | *Sapium sebiferum* | USA | EICA | Gr |
| Siemann and Rogers (2003a)[‡,§] | *Sapium sebiferum* | USA | FRA | B |
| Siemann and Rogers (2003b)[‡,§] | *Sapium sebiferum* | USA | ER | B, Ge, Gr, S |
| Siemann and Rogers (2003c)[‡,§] | *Sapium sebiferum* | USA | EICA | Gr |
| Siemann and Rogers (2003d)[‡,§] | *Sapium sebiferum* | USA | EICA | Gr, S |
| Siemann and Rogers (2006)[‡,§] | *Sapium sebiferum* | USA | ER | Ge, S |
| Siemann and Rogers (2007)[‡] | *Sapium sebiferum* | USA | FRA | – |
| Siemann et al. (2006)[‡,§] | *Sapium sebiferum* | USA | EICA | Gr, S |
| Siemann et al. (2007)[‡] | *Sapium sebiferum* | USA | FRA | – |
| Tecco et al. (2006)[‡,§] | *Ligustrum lucidum* | Argentina | F | DC |
| Tecco et al. (2007)[‡] | *Ligustrum lucidum* | Argentina | F | – |
| Vanhellemont et al. (2009) | *Prunus serotina* | Belgium | PP | – |
| Yamashita et al. (2002) | *Bischofia javanica* | Japan | FRA | – |
| Zalba et al. (2008) | *Pinus halepensis* | Argentina | D | – |
| Zou et al. (2006)[‡,§] | *Sapium sebiferum* | China | EICA | B, Gr, S |
| Zou et al. (2008a)[‡,§] | *Sapium sebiferum* | China | EICA | B, Gr, S |
| Zou et al. (2008b)[‡,§] | *Sapium sebiferum* | China | EICA | B, S |
| Zou et al. (2009)[‡,§] | *Sapium sebiferum* | USA | FRA | B, Gr, DC |

For each study, were respectively reported the invasive tree species studied, the study location, the hypothesis tested and the functional traits measured

[‡] Studies included in the meta-analysis conducted on hypotheses. [§] Studies included in the meta-analysis conducted on functional traits

[a] Disturbance, *EICA* evolution of increased competitive ability, *EN* empty niche, *ER* enemy release; *F* facilitation, *FRA* fluctuating resource availability, *NW* novel weapons (also called “allelopathy” hypothesis), *PP* propagule pressure

[b] Biomass, *Ge* germination, *Gr* growth rate, *DC* density/cover, *S* survival

The second meta-analysis was run to assess whether the functional traits equally promote tree invasiveness. Hence, control and treatment groups used here were mainly based on the comparison (1) between native and invasive populations of the invasive tree species studied or (2) between native species of the introduced range and the invasive tree species (see "Appendix 2"). We only compared functional traits that were widely studied as biomass (plant weight and root-shoot ratio), density/cover (number of trees or seedlings), germination (seed emergence, germination and seedling recruitment), growth rate (height and diameter increment) and survival. Lastly, effect sizes in a publication were pooled per species and per functional trait measured, and the pooled mean effect size and the mean variance were thus used. Consequently, the final data set included 80 studies reported in 41 publications encompassing 21 invasive trees (Table 1).

The meta-analytical calculations were performed using the program MetaWin 2 (Rosenberg et al. 2000). Confidence intervals (CI) of effect sizes were calculated using bootstrap resampling procedures (Adams et al. 1997) with 9999 iterations. The strength and pertinence of hypotheses and functional traits were evaluated according to *d* values and considered if the 95% biased-corrected bootstrap CI of the effect size *d* did not overlap zero (Rosenberg et al. 2000). Data were analyzed using random-effect models as it was assumed that, in addition to sampling error, there is a true random component of variation in effect sizes between studies (Gurevitch et al. 2001). Heterogeneity between hypotheses and between traits was examined with *Q*-statistics (Hedges and Olkin 1985) while publication bias was explored statistically with Spearman rank correlation test and examination of fail-safe numbers (Rosenberg 2005).

## Results

### Systematic review

A total of 6,308 articles were published that cited the eight main hypotheses advanced to explain biological invasions (Table 2). Nonetheless, within this set of publications, only 561 (9%) effectively tested these hypotheses on concrete cases of invasion, conducting experiments on invasive animal or plant species and for both terrestrial and aquatic communities. The most tested hypothesis on invasive species in general was the fluctuating resource availability hypothesis (16% of the 561 articles that effectively test any

**Table 2** Systematic review based on eight dominant hypotheses proposed to explain the success of invasive species

| Hypothesis | Article of reference | Time cited | Time tested on invasive sp | Time tested on invasive tree sp | | | |
|---|---|---|---|---|---|---|---|
| | | | | Total | Supported | Mixed | Rejected |
| D | Mack et al. (2000) | 1435 | 75 (13%) | 12 (13%) | 12 | 0 | 0 |
| EICA | Blossey and Notzold (1995) | 452 | 59 (10%) | 12 (13%) | 10 | 0 | 2 |
| EN | Levine and D'Antonio (1999) | 461 | 68 (12%) | 6 (7%) | 0 | 1 | 5 |
| ER | Keane and Crawley (2002) | 722 | 81 (14%) | 14 (16%) | 10 | 1 | 3 |
| F | Bruno et al. (2003) | 670 | 47 (8%) | 13 (14%) | 10 | 2 | 1 |
| FRA | Davis et al. (2000) | 1019 | 89 (16%) | 12 (13%) | 11 | 1 | 0 |
| NW | Callaway and Aschehoug (2000) | 429 | 73 (13%) | 9 (10%) | 6 | 0 | 3 |
| PP | Lonsdale (1999), Williamson and Fitter (1996) | 1120 | 69 (12%) | 12 (13%) | 11 | 1 | 0 |
| Total | | 6308 | 561 | 90 (16%) | 70 (78%) | 6 | 14 |

For each hypothesis, number of articles that respectively, cited it and tested it on both invasive species in general and invasive tree species in particular. The analysis of articles was conducted using the ISI Web of Science (date of access up to early November 2010). A vote-counting method was applied on the 96 articles that focused on invasive tree species. Percentages presented were calculated in function of the total number of articles of each column

See "Appendix 3" for more information on the invasive tree species studied

*D* disturbance, *EICA* evolution of increased competitive ability, *EN* empty niche, *ER* enemy release, *F* facilitation, *FRA* fluctuating resource availability, *NW* novel weapons (also called "allelopathy" hypothesis), *PP* propagule pressure hypothesis) whereas the facilitation hypothesis was the least tested (8%).

For invasive trees, a total of 90 observational and experimental studies concretely tested these hypotheses (Table 1). The most tested hypotheses in tree invasion ecology was the enemy release hypothesis (16% of the 90 articles that effectively test any hypothesis on invasive trees) while the least tested on invasive trees was also the empty niche hypothesis (8%; Table 2). A large proportion (78%) of articles focusing on invasive tree species reported support for the hypothesis they tested (Table 2). The empty niche hypothesis however found no support to explain tree invasions (Table 2; five articles rejected it and one had a mixed result).

A wide range of habitats, mainly open fields, grasslands and forests have been invaded by tree species in both Hemispheres and under temperate, subtropical and tropical climates (see "Appendix 3"). Invasion hypotheses were tested on different taxonomic groups including conifers, broadleaved evergreens and broadleaved deciduous species. Nonetheless, all the hypotheses were not tested in all systems and for example, studies conducted in the Southern Hemisphere on conifer tree invasions predominantly focused on the role of both propagule pressure and disturbance. Overall, there were 45 species of invasive trees from 23 different families studied in the 90 publications. However, invasive tree species were unequally represented among the studies with 17 species reported in only one study (see "Appendix 3"). In contrast, there were 11 articles that focused on conifer tree (Pinaceae family) invasions in the Southern Hemisphere, while in North America, there were 23 and 12 experiments that respectively tested invasion hypotheses on *Sapium sebiferum* (Chinese tallow tree) and *Acer platanoides* (Norway maple).

## Meta-analysis on hypotheses tested on invasive trees

The empty niche hypothesis was excluded from the comparison performed between hypotheses because too few studies were conducted to allow us to calculate an effect size. First, the overall weighted-mean effect size of this set of studies was positive ($d = 0.6889$) and significantly different from zero (95% bias-corrected bootstrap CI: 0.4956 to 0.9122; Fig. 1). We did not observe any difference in effect sizes between hypotheses related to invasibility and the ones linked to invasiveness ($d_{invasiveness} = 0.7073$, $d_{invasibility} = 0.6342$; $Q_{between} = 0.15$, $df = 1$, $P = 0.69$; Fig. 1). However, differences in effect sizes appeared between hypotheses. The novel weapons hypothesis only expressed an effect size greater than 1 ($d_{NW} = 1.7717$). While the propagule pressure and the facilitation hypotheses had also relative large effect sizes ($d_{PP} = 0.9582$, $d_F = 0.9194$), the four other hypotheses showed moderate effect sizes ($d_{EICA} = 0.6469$, $d_D = 0.5647$, $d_{FRA} = 0.4654$ and $d_{ER} = 0.3735$; Fig. 1). Further analysis revealed that the novel weapons hypothesis expressed a significant greater effect size than the other hypotheses ($Q_{between} = 13.31$, $df = 1$, $P = 0.0003$). When running the meta-analysis without studies related to the novel weapons hypothesis, no significant difference was found between effect sizes ($Q_{between} = 5.32$, $df = 5$, $P = 0.38$).

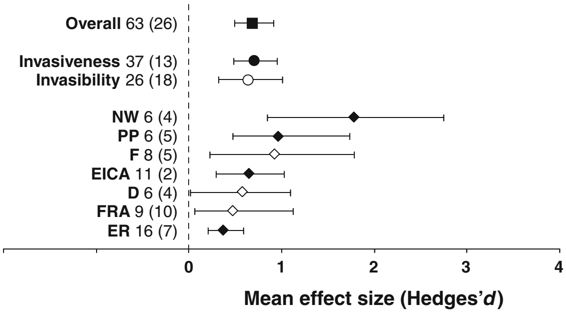

**Fig. 1** Weighted-mean effect sizes (Hedges' *d*) and 95% bias-corrected confidence intervals calculated for seven dominant hypotheses proposed to explain invasion in trees (the effect size could not be calculated for the empty niche hypothesis). The number of studies and, in parentheses, the number of invasive tree species they refer to, are given on the *left-hand side* of the graph; *dotted line* shows Hedge's $d = 0$. *Black* and *white* effect sizes refer respectively to hypotheses linked to invasiveness and invasibility. *Abbreviations* are as specified in Table 1

## Meta-analysis on functional traits measured in invasive tree studies

The grand mean effect size for all the functional traits was positive ($d = 0.5945$) and significantly different from zero (95% bias-corrected bootstrap CI: 0.3970 to 0.7975; Fig. 2). The heterogeneity of effect sizes was not statistically significant ($Q_{between} = 6.45$, $df = 4$, $P = 0.16$; Fig. 2). Nevertheless, growth rate showed the largest effect size ($d_{growth\ rate} = 0.9217$) while the effect size values were moderate for

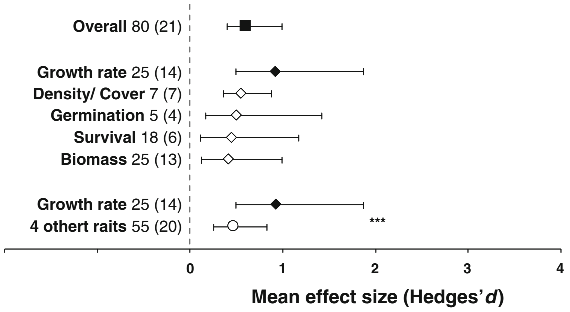

**Fig. 2** Weighted-mean effect sizes (Hedges' $d$) and 95% bias-corrected confidence intervals calculated for the five main functional traits used in invasive tree species. The number of studies and, in parentheses, the number of invasive tree species they refer to, are given on the *left-hand side* of the graph; *dotted line* shows Hedge's $d = 0$. Significant levels associated with $Q$-values: $^{***}P < 0.05$

density/cover, germination, biomass and survival ($d_{density/cover} = 0.5292$, $d_{germination} = 0.4913$, $d_{survival} = 0.4505$ and $d_{biomass} = 0.4046$). Further analysis hence revealed a significant difference between growth rate and the four other functional traits pooled together ($Q_{between} = 6.49$, $df = 1$, $P = 0.01$; Fig. 2). When we re-analysed the studies linked to all the functional traits except growth rate, no significant difference was found between effect sizes ($Q_{between} = 0.19$, $df = 3$, $P = 0.97$).

### Publication bias

The inspection of the weighted histogram of effect sizes of the raw data showed no depression around zero and the funnel plot of the effect sizes *versus* the sample size did not show skewness suggesting no publication bias in reporting results from the studies included in this meta-analysis (Aguilar et al. 2006). The robustness of our results was also supported by Rosenthal's weighted fail-safe number (51,408.4) which was much greater than the number of studies (6840) expected without publication bias (Rosenberg et al. 2000).

## Discussion

In this study, a quantitative review and meta-analytical statistics were used to summarize the progress to date in understanding tree invasions. Importantly, seven of the eight hypotheses prevalent in the grassland invasion literature also apply to invasive tree species. Because it was more often rejected, the empty niche hypothesis may be the least relevant hypothesis. In addition, although all the functional traits tested were identified as determinants of tree invasiveness, growth rate was the most significant. Invasions by trees were explained by the same hypotheses that have been successfully applied to invasive grass species, which suggests that similar processes may function, at least coarsely, in forests and grasslands with respect to factors that promote the success of introduced species.

To date, 90 publications have concretely tested the eight dominant invasion hypotheses on invasive tree species, encompassing a total of 45 non-indigenous tree species that are proliferating in their introduced range. Studies were mostly conducted in South Africa on conifer and evergreen trees and in North America on invasive deciduous trees. Most of these studies (69) were published within the last 5 years, which clearly indicates the growing interest for invasive trees within plant invasion ecology. However, all the tree species were not equally studied and some tree species dominate the literature to date, which can partially explain the geographical and taxonomic biases in invasion ecology highlighted by Pysek et al. (2008). *Pinus* and *Acacia* spp. invasions into grasslands and shrublands represent the most extensive research on invasive trees in the Southern Hemisphere (Higgins and Richardson 1998; Rouget et al. 2001; Alston and Richardson 2006; Dezzotti et al. 2009) while in North America, broadleaved deciduous *Acer platanoides* invasion into forests and *Sapium sebiferum* invasion into coastal prairies feature the dominant cases of invasive trees studied in the Northern Hemisphere (Conway et al. 2002; Barton et al. 2004; Morrison and Mauck 2007; Battaglia et al. 2009). Consequently, more research efforts on a broader pool of invasive trees are still necessary to fully understand the broad processes that promote tree invasions, particularly since 357 tree species are considered invasive in at least one region of the world (Richardson and Rejmanek, in press).

Hypotheses linked to invasiveness and the ones linked to invasibility equally contribute to explaining tree invasions. With the exception of the empty niche hypothesis (see below), the systematic review revealed that the dominant hypotheses for plant invasions were successfully tested on invasive trees

(100% for invasiveness hypotheses and 75% for invasibility hypotheses), whilst the meta-analysis conducted on the hypotheses similarly showed that they all generated significant positive effect sizes. These findings lead to two key conclusions. First, tree invasions cannot be explained by a single hypothesis and are likely related to changes in several biological factors in the invaded habitats. Indeed, invasiveness and invasibility interact in trees to promote invasion processes (Richardson and Pysek 2006). Hence, the success of invasive trees appears to be context-dependent. For instance, species adapted to high resource availability are also those most affected by natural enemies in their native range (Blumenthal 2006; Blumenthal et al. 2009). When introduced to a new region, they benefit more from both enemy release and resource availability than well-defended species adapted to low resource availability (Blumenthal 2005). Second, several hypotheses were successfully tested on the same invasive tree species, which further suggests that no one mechanism may fully explain invasion into forests. For instance, in the case of *Sapium sebiferum* in wetland and upland habitats of the United States, studies suggested that various mechanisms such as loss of natural enemies, evolutionary shifts in resource allocation, use of allelopathic components and changes in light and nitrogen availability may promote its high and ongoing invasion of grasslands (Siemann and Rogers 2003b, 2007; Zou et al. 2008a, 2009). Evidence from these experiments supports recent findings that species attributes and attributes of recipient communities interact during plant invasion events (Krivanek et al. 2006; Pysek and Richardson 2007; Pysek et al. 2009).

However, all the hypotheses might not equally explain tree invasions. Results from the systematic review showed that the majority of the studies supported the hypothesis they tested, except for the empty niche hypothesis. Given that no single study reported support for it (Howard et al. 2004; Belote et al. 2008), the empty niche hypothesis is the least relevant hypothesis for invasive tree success. This may be due to the concept of empty niche itself. With local and regional factors as determinants of forest invasibility (Knight and Reich 2005; Ohlemüller et al. 2006), the empty niche hypothesis seems too vague and less precisely defined than the ideas supported by the other hypotheses. Nonetheless, few studies only tested this hypothesis on invasive trees to date, which prevented us from including it in the meta-analysis, and consequently, more research is crucial to test its consistency. Conversely, the novel weapons hypothesis, which showed a very large positive effect size, suggests that tree invasion is successful when exotic trees are able to release allelopathic compounds, as shown for *Sapium sebiferum* in North America and *Acacia dealbata* in Europe (Keay et al. 2000; Lorenzo et al. 2010b). The facilitation theory also showed a large effect size and thus presents a new direction for research in tree invasions. Interestingly, various facilitative effects were described by the experimental studies that successfully tested this hypothesis to date. For example, establishment or regeneration of invasive tree seedlings can be facilitated by adult conspecifics and soil pathogens (Reinhart et al. 2005, 2006) and native or non-native woody species (Tecco et al. 2007; Iponga et al. 2010). In addition, the theory of facilitation can also be closely related to other processes promoting tree invasions such as disturbance (Richardson et al. 1994; Alston and Richardson 2006; Carvalho et al. 2010) or enemy release (Reinhart and Callaway 2004; Adams et al. 2009; Reinhart et al. 2010). Moreover, propagule pressure, usually seen as a key factor of plant invasion (Lockwood et al. 2009), has been quantitatively recognized as a significant characteristic of invasion in trees (Richardson 1998; Kaproth and McGraw 2008; Pysek et al. 2009; Martin and Canham 2010), and thus needs to be integrated as a basis of a null model when studying process of tree invasion (Rouget and Richardson 2003; Colautti et al. 2006). Finally, our results also emphasized the importance of both phenotypic plasticity, commonly linked to the enemy release hypothesis, and genetic adaptation, supported by the EICA hypothesis. Tested on a relative large number of invasive trees, the enemy release hypothesis has been supported in general, particularly with invasive species and populations experiencing less herbivore damage than native species of the introduced range or native populations (Lankau et al. 2004; Cincotta et al. 2009), which is consistent with previous meta-analyses on herbivore loads and invasive plant species (Maron and Vila 2001; Liu and Stiling 2006). As for the EICA hypothesis, it was also supported through genetic evolution in invasive trees with positive and significant effect sizes detected here (Siemann and Rogers 2001; Rogers and Siemann 2004). However, because it has been soundly tested but on only a single species, *Sapium sebiferum*, more experimental studies on other tree species are needed before we can make any definitive conclusions about the role of genetic evolution of tree populations in their invasive success. In addition, in order to fully interpret the global effects of the EICA hypothesis, invasive and native populations need to be tested in more than one environment concurrently and in both native and invasive ranges (Williams et al. 2008), which has not yet been conducted for invasive tree species to date.

All the five functional traits showed positive effect sizes, and consequently can be identified as determinants of tree invasiveness. This result is in accordance with a recent meta-analysis conducted by van Kleunen et al. (2010), where invasive alien species were found to have significant greater values for six performance-related traits than non-native species. In addition, the most interesting finding of our study is that growth rate, independently of the experimental treatment applied, is an important and dominant measure in tree invasions relative to survival, density, biomass and germination. Thus, growth rate appears not only to be the key functional trait linked to invasiveness for a tree species but also to be the most associated with the invasion success of tree species once established. This is in agreement with a previous study that identified the relative growth rate as the most important predictor of invasiveness in disturbed habitats for 29 pines species (Grotkopp et al. 2002) and supports the hypothesis that stem elongation is assumed to enhance fitness by improving plant competitive ability for resources (Baruch et al. 2000; Closset-Kopp et al. 2010). In contrast, previous findings on weed species in grasslands showed that invasive species are better characterized by high germination rates rather than high growth rates (Milbau et al. 2003). Hence, trees may be unique relative to weed species in grasslands with respect to the relative importance of growth rate over other performance-related traits and, in consequence, growth rate should be more frequently used in future tree invasion studies. Maximum assimilation rate ($A_{\max}$) and specific leaf area (SLA) have been identified as the most significant factors affecting relative growth rate (Swanborough and Westoby 1996; Hoffmann and Poorter 2002). Given that it also represents an easy, fast and inexpensive measurement, SLA could become an efficient diagnostic tool when assessing and comparing growth performances between native and invasive tree species. For instance, some previous studies have already emphasized the benefit of higher SLA and higher net $CO_2$ assimilation for invasive species over native neighbours (Baruch and Goldstein 1999; Feng et al. 2007). Nonetheless, because Rejmánek and Richardson (1996) were able to explain invasiveness in *Pinus* species using only three other traits without growth (seed mass, length of juvenile period and interval between seed mast years), quantitative measures of other functional traits are also necessary. While data are more available for tree growth and biomass as evidenced in the present study, data are scarcer on dispersal and reproduction, although these factors are crucial for invasion success (Rejmánek et al. 2005; Martin and Canham 2010). Consequently, although flowering, seed production and dispersal are hard to investigate in long-lived trees, further efforts need to focus on these reproductive traits before we could consider these conclusions as definitive.

In conclusion, both invasiveness and invasibility are involved in the expansion of exotic tree species, as previously reported for invasive grass species. Our results indeed indicate that several factors can simultaneously act to explain the success of invasive trees. In addition, although a remarkably great number of tree species are reported as invasive all over the world, few studies have focused on this taxon compared to other taxa (grass and animal) and further research is needed, especially on poorly studied broad-scale invaders such as *Acacia mearnsii* and *Leucaena leucocephala* (Richardson and Rejmanek, in press).

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## Appendix 1

See Table 3.

**Table 3** Control and treatment data for all the studies included in the meta-analysis conducted on the invasion hypotheses

| References | Hypothesis | Control | Treatment |
|---|---|---|---|
| Adams et al. (2009) | ER | Invasive sp./native range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Bellingham et al. (2005) | EN | Invasive sp./invasive range/before hurricane | Invasive sp./invasive range/after hurricane |
| Carvalho et al. (2010) | D | Invasive sp./invasive range/unburned field | Invasive sp./invasive range/burned field |
| Chaneton et al. (2004) | D | Invasive sp./invasive range/unburned field | Invasive sp./invasive range/burned field |
| Cincotta et al. (2009) | ER | Native sp./invasive range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Donnelly and Walters (2008) | PP | Invasive sp./invasive range/0 ppt salt saltwater | Invasive sp./invasive range/15 or 30 ppt saltwater |
| Donnelly et al. (2008) | NW | Native sp./invasive range/no *Schinus* fruits | Native sp./invasive range/*Schinus* fruits |
| Franks et al. (2008a) | EICA | Invasive sp./native population/insecticide resistance | Invasive sp./invasive population/insecticide resistance |
| Green et al. (2004) | ER | Invasive sp./invasive range/seedlings uncaged | Invasive sp./invasive range/seedlings caged |
| Huang et al. (2010) | EICA | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Iponga et al. (2009a) | PP | Invasive sp./invasive range/ungrazed savanna | Invasive sp./invasive range/grazed savanna |
| Iponga et al. (2009b) | F, ER | Invasive sp./invasive range/with herbivory | Invasive sp./invasive range/without herbivory |
| Iponga et al. (2010) | F | Invasive sp./invasive range/under native sp. | Invasive sp./invasive range/under non-native sp. |
| Kaproth and McGraw (2008) | PP | Invasive sp./invasive range/terrestrial conditions | Invasive sp./invasive range/aqueous conditions |
| Knapp et al. (2008) | ER | Invasive sp./invasive range/herbivore exclosure | Invasive sp./invasive range/no herbivore exclosure |
| Lankau et al. (2004) | ER | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Lesica and DeLuca (2004) | NW | Native sp./invasive range/outside | Native sp./invasive range/under Tamarix canopy |
| Liu et al. (2007) | ER | Native sp./invasive range/predation resistance | Invasive sp./invasive range/predation resistance |
| Lockhart et al. (1999) | FRA | Invasive sp./invasive range/no water level | Invasive sp./invasive range/high water level |
| Lorenzo et al. (2008) | NW | Native sp./invasive range/no *Acacia* extracts | Native sp./invasive range/*Acacia* extracts |
| Lorenzo et al. (2010a, b) | NW | Native sp./invasive range/no *Acacia* extracts | Native sp./invasive range/*Acacia* extracts |
| Martin and Canham (2010) | PP | Native sp./invasive range/seed production | Invasive sp./invasive range/seed production |
| Martin and Marks (2006) | FRA | Invasive sp./invasive range/shade | Invasive sp./invasive range/light |
| Mazia et al. (2001) | D | Invasive sp./invasive range/litter intact | Invasive sp./inv. range/litter removed |
| Mazia et al. (2010) | D | Invasive sp./invasive range/unburning and no armadillo | Invasive sp./invasive range/burning and armadillo |
| McCay and McCay (2009) | PP | Invasive sp./invasive range/no perch | Invasive sp./inv. range/perch |
| Morgan and Overholt (2005) | NW | Native sp./invasive range/distilled water | Native sp./invasive range/*Schinus* extracts |
| Morrison and Mauck (2007) | ER | Invasive sp./invasive range/seedlings caged | Invasive sp./invasive range/seedlings uncaged |
| Nasir et al. (2005) | NW | Native sp./invasive range/no *Robinia* extracts | Native sp./invasive range/*Robinia* extracts |
| Nijjer et al. (2007) | F | Invasive sp./native population/soil treatments | Invasive sp./invasive population/soil treatments |
| Peperkorn et al. (2005) | FRA | Invasive sp./invasive range/no light and nutrient | Invasive sp./invasive range/light and nutrient |
| Reinhart and Callaway (2004) | ER | Invasive sp./native range/conspecific soil | Invasive sp./invasive range/conspecific soil |
| Reinhart et al. (2003) | ER | Invasive sp./native range/conspecific soil | Invasive sp./invasive range/conspecific soil |
| Reinhart et al. (2005) | F | Invasive sp./under native canopy | Invasive sp./under non-native canopy |
| Reinhart et al. (2006) | F | Invasive sp./invasive range/uninvaded patch | Invasive sp./invasive range/invaded patch |
| Reinhart et al. (2010) | ER | Invasive sp./native soil pathogen | Invasive sp./non-native soil pathogen |
| Relva et al. (2010) | F | Invasive sp./seedling caged | Invasive sp./seedling uncaged |

**Table 3** continued

| References | Hypothesis | Control | Treatment |
|---|---|---|---|
| Rogers and Siemann (2002) | ER | Native sp./invasive range/resources and herbivory | Invasive sp./invasive range/resources and herbivory |
| Rogers and Siemann (2003) | ER | Invasive sp./invasive range/resources and herbivory | Invasive sp./invasive range/resources and no herbivory |
| Rogers and Siemann (2004) | EICA | Invasive sp./native range/resource availability | Invasive sp./invasive range/resource availability |
| Rogers and Siemann (2005) | EICA | Invasive sp./native range/resource and herbivory | Invasive sp./invasive range/resource and herbivory |
| Schumacher et al. (2008) | FRA | Invasive sp./invasive range/low resource level | Invasive sp./invasive range/high resource level |
| Schumacher et al. (2009) | FRA | Invasive sp./invasive range/low resource level | Invasive sp./invasive range/high resource level |
| Siemann and Rogers (2001) | EICA | Invasive sp./native population seeds | Invasive sp./invasive population seeds |
| Siemann and Rogers (2003a) | FRA | Invasive range/native sp./resource level | Invasive range/invasive sp./resource level |
| Siemann and Rogers (2003b) | ER | Native sp./invasive range/disease resistance | Invasive sp./invasive range/disease resistance |
| Siemann and Rogers (2003c) | EICA | Invasive sp./native population seedlings | Invasive sp./invasive population seedlings |
| Siemann and Rogers (2003d) | EICA | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Siemann and Rogers (2006) | ER | Native sp./invasive range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Siemann and Rogers (2007) | FRA | Invasive sp./invasive range/low resource level | Invasive sp./invasive range/high resource level |
| Siemann et al. (2006) | EICA | Invasive sp./native population seedlings | Invasive sp./invasive population seedlings |
| Siemann et al. (2007) | FRA | Invasive sp./invasive range/water treatment | Invasive sp./invasive range/water treatment |
| Tecco et al. (2006) | F | Invasive sp./invasive range/shrub cover | Invasive sp./invasive range/no shrub cover |
| Tecco et al. (2007) | F | Invasive sp./invasive range/shrub cover | Invasive sp./invasive range/no shrub cover |
| Zou et al. (2006) | EICA | Invasive sp./native population/resource availabiity | Invasive sp./invasive population/resource availability |
| Zou et al. (2008a) | EICA | Invasive sp./native population/resource availability | Invasive sp./invasive population/resource availability |
| Zou et al. (2008b) | EICA | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Zou et al. (2009) | FRA | Invasive sp./invasive range/light and N treatment | Invasive sp./invasive range/light and N treatment |

Mean value, sample size and error term of both control and treatment were used to calculate Hedges' *d*

*D* disturbance, *EICA* evolution of increased competitive ability, *EN* empty niche, *ER* enemy release, *F* facilitation, *FRA* fluctuating resource availability, *NW* novel weapons (also called "allelopathy" hypothesis)

## Appendix 2

See Table 4.

**Table 4** Control and treatment data for all the studies included in the meta-analysis conducted on the functional traits

| References | Trait category | Control | Treatment |
|---|---|---|---|
| Adams et al. (2009) | S | Invasive sp./native range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Bellingham et al. (2005) | DC | Native sp./invasive range/after hurricane | Invasive sp./invasive range/after hurricane |
| Carvalho et al. (2010) | B | Native sp./invasive range/unburned field | Invasive sp./invasive range/unburned field |
| Chaneton et al. (2004) | B, Ge, S | Invasive sp./invasive range/unburned field | Invasive sp./invasive range/burned field |
| Cincotta et al. (2009) | B, S | Native sp./invasive range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Franks et al. (2008a) | B, Gr | Invasive sp./native population/insecticide resistance | Invasive sp./invasive population/insecticide resistance |
| Huang et al. (2010) | B, Gr | Invasive sp/native population/herbivory resistance | Invasive sp/invasive population/herbivory resistance |
| Knapp et al. (2008) | Gr, S | Native sp./invasive range/herbivore exclosure | Invasive sp./invasive. range/no herbivore exclosure |
| Lankau et al. (2004) | B, S | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |

**Table 4** continued

| References | Trait category | Control | Treatment |
|---|---|---|---|
| Leger et al. (2007) | B | Native sp./invasive range/soil nutrients | Invasive sp./invasive range/soil nutrients |
| Liu et al. (2007) | Ge, S | Native sp./invasive range/predation resistance | Invasive sp./invasive range/predation resistance |
| Lorenzo et al. (2010a, b) | Ge, Gr | Native sp./invasive range/no *Acacia* extracts | Native sp./invasive range/*Acacia* extracts |
| Martin and Canham (2010) | DC | Native sp./invasive range/seed production | Invasive sp./invasive range/seed production |
| Mazia et al. (2010) | S | Invasive sp./invasive range/unburning and no armadillo | Invasive sp./invasive range/burning and armadillo |
| McCay and McCay (2009) | DC, S | Invasive sp./invasive range/no perch | Invasive sp./inv. range/perch |
| Morrison and Mauck (2007) | B, Gr, S | Native sp./invasive range/seedlings caged | Invasive sp./invasive range/seedlings uncaged |
| Nijjer et al. (2007) | B, Gr, S | Invasive sp./native population/soil treatments | Invasive sp./invasive population/soil treatments |
| Peperkorn et al. (2005) | B, Gr | Native sp./invasive range/no light and nutrient | Invasive sp./invasive range/light and nutrient |
| Reinhart and Callaway (2004) | B, Gr | Invasive sp./native range/conspecific soil | Invasive sp./invasive range/conspecific soil |
| Reinhart et al. (2003) | B | Invasive sp./native range/conspecific soil | Invasive sp./invasive range/conspecific soil |
| Reinhart et al. (2005) | B, Gr | Native sp./invasive range/under native canopy | Invasive sp./invasive range/under native canopy |
| Reinhart et al. (2010) | B, S | Invasive sp./native soil pathogen | Invasive sp./non-native soil pathogen |
| Relva et al. (2010) | DC, Gr | Native sp./invasive range | Invasive sp./invasive range |
| Reynolds and Cooper (2010) | Gr | Native sp./invasive range/light and water treatment | Invasive sp./invasive range/light and water treatment |
| Rogers and Siemann (2002) | Gr, | Native sp./invasive range/resources and herbivory | Invasive sp./invasive range/resources and herbivory |
| Rogers and Siemann (2004) | B, Gr | Invasive sp./native range/resource availability | Invasive sp./invasive range/resource availability |
| Rogers and Siemann (2005) | B, Gr | Invasive sp./native range/resource and herbivory | Invasive sp./invasive range/resource and herbivory |
| Schumacher et al. (2008) | B, Gr | Native sp./invasive range/low resource level | Invasive sp./invasive range/high resource level |
| Schumacher et al. (2009) | B, Gr | Native sp/invasive range/low resource level | Invasive sp/invasive range/high resource level |
| Siemann and Rogers (2001) | Gr | Invasive sp./native population seeds | Invasive sp./invasive population seeds |
| Siemann and Rogers (2003a) | B | Invasive range/native sp./resource level | Invasive range/invasive sp./resource level |
| Siemann and Rogers (2003b) | B, Ge, Gr, S | Native sp/invasive range/disease resistance | Invasive sp/invasive range/disease resistance |
| Siemann and Rogers (2003c) | Gr | Invasive sp./native population seedlings | Invasive sp./invasive population seedlings |
| Siemann and Rogers (2003d) | Gr, S | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Siemann and Rogers (2006) | Ge, S | Native sp./invasive range/herbivory resistance | Invasive sp./invasive range/herbivory resistance |
| Siemann et al. (2006) | Gr, S | Invasive sp./native population seedlings | Invasive sp./invasive population seedlings |
| Tecco et al. (2006) | DC | Native sp/invasive range | Invasive sp/invasive range |
| Zou et al. (2006) | B, Gr, S | Invasive sp./native population/resource availability | Invasive sp./invasive population/resource availability |
| Zou et al. (2008a) | B, Gr, S | Invasive sp./native population/resource availability | Invasive sp./invasive population/resource availability |
| Zou et al. (2008b) | B, S | Invasive sp./native population/herbivory resistance | Invasive sp./invasive population/herbivory resistance |
| Zou et al. (2009) | B, Gr, DC | Invasive sp./native population/light and N treatment | Invasive sp./invasive population/light and N treatment |

Mean value, sample size and error term of both control and treatment were used to calculate Hedges' *d*

*B* biomass, *Ge* germination, *Gr* growth rate, *DC* density/cover, *S* survival

## Appendix 3

See Table 5.

**Table 5** List of the invasive tree species studied in the 96 articles selected from the systematic review

| Invasive tree sp | Family | Growth form | Native range | | Introduced range | | Invaded habitat | Study location |
|---|---|---|---|---|---|---|---|---|
| | | | Location | Climate | Location | Climate | | |
| *Acacia cyclops* | Mimosaceae | Broadl ev | S Aus, W Aus | Temp | SA | Temp | Shrubl | SA |
| *Acacia dealbata* | Mimosaceae | Broadl ev | SE Aus | Temp | S Eur | Temp | Open, for | Spa |
| *Acacia longifolia* | Mimosaceae | Broadl ev | SE Aus | Temp | SA, Por | Temp | Sand, shrubl, for | Por, Ger, SA |
| *Acacia saligna* | Mimosaceae | Broadl ev | SW Aus | Temp | SA | Temp | Shrubl, for | SA |
| *Acer negundo* | Aceraceae | Broadl dec | N Am | Temp | Eur | Temp | Dist, rip hab | USA, Fra, CZ |
| *Acer platanoides* | Aceraceae | Broadl dec | Eur | Temp | NE Am | Temp | For | USA, Eur |
| *Adenanthera pavonia* | Fabaceae | Broadl dec | India, SE Asia | Trop | Ams, Pac Is | Trop | Coastl, dist, for | Aus |
| *Ailanthus altissima* | Simaroubaceae | Broadl dec | China | Temp/subtr | USA, SE Eur, Aus, NZ | Temp/subtrop | Dist, open, for | USA, CZ |
| *Alstonia macrophylla* | Apocynaceae | Broadl ev | SE Asia | Trop | Ind Is, Pac Is | Trop | For | Seychelles |
| *Bischofia javanica* | Euphorbiaceae | Broadl ev | SE Asia, Aus, Pac Is | Trop | Jap | Subtrop | For | Jap |
| *Cinnamomum verum* | Lauraceae | Broadl ev | Asia | Trop | Ind Is, Pac Is | Trop | For | Seychelles |
| *Elaeagnus angustifolia* | Elaeagnaceae | Broadl dec | E Eur, Asia | Temp/subtr | S USA | Temp/subtrop | For | USA |
| *Eriobotrya japonica* | Rosaceae | Broadl ev | SE Asia | Temp | N Am, Med Bas, SA | Temp | For | SA |
| *Eugenia uniflora* | Myrtaceae | Broadl ev | Bra | Trop | SE USA | Subtrop | For | USA |
| *Gleditsia triacanthos* | Fabaceae | Broadl dec | E N Am | Temp | Arg, Eur, SA, Aus | Temp | Grassl, for | Arg |
| *Homalanthus populifolius* | Euphorbiaceae | Broadl ev | E Aus | Temp | SA, NZ, HI | Temp | For | SA |
| *Ligustrum lucidum* | Oleaceae | Broadl ev | E Asia | Temp | USA, Arg, S Af, Aus, NZ | Temp | Grassl, for | Arg |
| *Melaleuca quinquenervia* | Myrtaceae | Broadl ev | E Aus, NGui, NCal | Temp/subtr | SE USA | Subtrop | Grassl, shrubl, for | USA |
| *Paraserianthes lophantha* | Fabaceae | Broadl ev | SW Aus | Temp | S Am, S Af, NZ, HI | Temp | For | SA |
| *Paulownia tomentosa* | Scrophulariaceae | Broadl dec | Asia | Temp | USA | Temp | For | USA |
| *Pinus canariensis* | Pinaceae | Conifer | Canary Is | Temp | W USA, SA, Aus | Temp | shrubl, for | SA |
| *Pinus halepensis* | Pinaceae | Conifer | Med Bas | Temp | S Am, S Af, Aus, NZ | Temp | Grassl, shrubl, for | Arg, SA |
| *Pinus pinaster* | Pinaceae | Conifer | W Eur, N Af | Temp | SA | Temp | Shrubl, for | SA |
| *Pinus ponderosa* | Pinaceae | Conifer | W NA | Temp | S Am, SA, Aus, NZ | Temp | Grassl, shrubl, for | Arg |
| *Pinus radiata* | Pinaceae | Conifer | W NA | Temp | S Am, SA, Aus, NZ | Temp | Grassl, shrubl | Arg, SA |
| *Pinus strobus* | Pinaceae | Conifer | NA | Temp | Eur, SA | Temp | Grassl, shrubl, for | CZ, SA |
| *Pittosporum undulatum* | Pittosporaceae | Broadl ev | SE Aus | Subtr | Car Is, S Bra, Az Is, SA | Temp/subtrop | For | Jam, SA |
| *Populus x canescens* | Salicaceae | Broadl dec | Eur | Temp | N Am, SH | Temp | For | SA |
| *Prosopis caldenia* | Fabaceae | broadl ev | S Am | Temp | Arg | Temp | Grassl, for | Arg |

**Table 5** continued

| Invasive tree sp | Family | Growth form | Native range | | Introduced range | | Invaded habitat | Study location |
|---|---|---|---|---|---|---|---|---|
| | | | Location | Climate | Location | Climate | | |
| *Prunus serotina* | Rosaceae | Broadl dec | N Am | Temp | Eur | Temp | Grassl, for | USA, Fra, Bel, Hol, CZ, Pol, |
| *Pseudotsuga menziesii* | Pinaceae | Conifer | W N Am | Temp | W Eur, SA | Temp | For | Arg |
| *Psidium cattleianum* | Myrtaceae | Broadl ev | S Am | Trop | Ind Is, Pac Is | Trop | For | Seychelles |
| *Quercus robur* | Fagaceae | Broadl dec | Eur, N Af, W Asia | Temp | N Am, SA | Temp | For | SA |
| *Quercus rubra* | Fagaceae | Broadl dec | E N Am | Temp | Eur | Temp | For | CZ |
| *Rhamnus cathartica* | Rhamnaceae | Broadl dec | Eur, W Asia | Temp | N Am | Temp | Open, for | USA |
| *Robinia pseudo-acacia* | Fabaceae | Broadl dec | SE USA | Temp | Eur, S Af, Asia | Temp | Dist, for | USA, CZ, Jap |
| *Sandoricum koetjape* | Meliaceae | Broadl ev | SE Asia | Trop | Ind Is, Pac Is | Trop | For | Seychelles |
| *Sapium sebiferum* | Euphorbiaceae | Broadl dec | E China | Temp/subtr | SE USA | Temp/subtrop | Grassl, coast pr | USA, China |
| *Schinus molle* | Anarcadiaceae | Broadl ev | S Am | Arid | S USA, SA, Aus | Arid | Grassl, for | SA |
| *Schinus terebinthifolius* | Anarcadiaceae | Broadl ev | S Am | Subtr/trop | S USA, S Af, Ind Is, Pac Is | Subtrop | Grassl, for | USA |
| *Solanum mauritianum* | Solanaceae | Broadl ev | S Am | Temp/trop | S Af, Ind Is, Aus, NZ, Pac Is | Temp/trop | For | SA |
| *Syzygum jambos* | Myrtaceae | Broadl ev | SE Asia | Trop | C Am, Ind Is, Aus, Pac Is | Trop | For | Seychelles |
| *Tabebuia pallida* | Bigogniaceae | Broadl ev | Lesser Antilles | Trop | Ind Is | Trop | For | Seychelles |
| *Tamarix ramosissima* | Tamaricaceae | Broadl dec | E Eur, Asia | Temp | USA, Arg, SA, Aus | Temp | For | USA |
| *Ulmus pumila* | Ulmaceae | Broadl dec | E Si, N China, Kor | Temp | USA, Mex, Arg | Temp | Grassl, for | Arg |

For each tree species, were respectively reported their family and growth form, the location and climate of its native and introduced ranges, its invaded habitat and the study location. All the tree species listed here are reported as invasive species in the location of the corresponding article

Abbreviations are as follow: **Growth form** *broadl* broadleaved, *dec* deciduous, *ev* evergreen. **Climate** *temp* temperate, *trop* tropical, *subtr* subtropical. **Location** *Af* Africa, *Am* America, *Ams* Americas, *Arg* Argentina, *Aus* Australia, *Az* Azores, *Bel* Belgium, *Bra* Brazil, *C* Central, *Car* Caribbean, *CZ* Czech Republic, *E* East, *Eur* Europe, *Fra* France, *Ger* Germany, *HI* Hawaii, *Hol* Holland, *Is* Islands, *Ind* Indian Ocean, *Jam* Jamaica, *Jap* Japan, *Kor* Korea, *Med Bas* Mediterranean Basin, *Mex* Mexico, *N* North, *NGui* New Guinea, *NCal* New Caledonia, *Pac* Pacific, *Pol* Poland, *Por* Portugal, *S* South, *SA* Republic of South Africa, *SH* South Hemisphere, *Si* Siberia, *Spa* Spain, *USA* United States of America, *NZ* New Zealand, *W* West. **Invaded habitat** *coast pr* coastal prairies, *dist* disturbed areas, *for* forest, *grassl* grasslands, *open* open fields, *rip hab* riparian habitats, *sand* sand dunes, *shrubl* shrublands

## References

Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling tests for meta-analysis of ecological data. Ecology 78:1277–1283

Adams JM, Fang W, Callaway RM, Cipollini D, Newell E (2009) A cross-continental test of the enemy release hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. Biol Invasions 11:1005–1016

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980

Alston KP, Richardson DM (2006) The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. Biol Conserv 132:183–198

Barton AM, Brewster LB, Cox AN, Prentiss NK (2004) Nonindigenous woody invasive plants in a rural New England town. Biol Invasions 6:205–211

Baruch Z, Goldstein G (1999) Leaf construction cost, nutrient concentration, and net $CO_2$ assimilation of native and invasive species in Hawaii. Oecologia 121:183–192

Baruch Z, Pattison RR, Goldstein G (2000) Responses to light and water availability of four invasive Melastomataceae in the Hawaiian islands. Int J Plant Sci 161:107–118

Battaglia LL, Denslow JS, Inczauskis JR, Baer SG (2009) Effects of native vegetation on invasion success of Chinese tallow in a floating marsh ecosystem. J Ecol 97:239–246

Bellingham PJ, Tanner EVJ, Healey JR (2005) Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. J Veg Sci 16:675–684

Belote RT, Jones RH (2009) Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms. Biol Invasions 11:1045–1052

Belote RT, Jones RH, Hood SM, Wender BW (2008) Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. Ecology 89:183–192

Blackburn TM, Jeschke JM (2009) Invasion success and threat status: two sides of a different coin? Ecography 32:83–88

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants—a hypothesis. J Ecol 83:887–889

Blumenthal D (2005) Ecology—interrelated causes of plant invasion. Science 310:243–244

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecol Lett 9:887–895

Blumenthal D, Mitchell CE, Pysek P, Jarosik V (2009) Synergy between pathogen release and resource availability in plant invasion. Proc Natl Acad Sci 106:7899–7904

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–125

Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523

Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? Trends Ecol Evol 21:369–374

Carvalho LM, Antunes PM, Martins-Loucao MA, Klironomos JN (2010) Disturbance influences the outcome of plant-soil biota interactions in the invasive *Acacia longifolia* and in native species. Oikos 119:1172–1180

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest. Divers Distrib 14:204–212

Chaneton EJ, Mazia CN, Machera M, Uchitel A, Ghersa CM (2004) Establishment of honey locust (*Gleditsia triacanthos*) in burned Pampean grasslands. Weed Technol 18:1325–1329

Cincotta CL, Adams JM, Holzapfel C (2009) Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). Biol Invasions 11:379–388

Closset-Kopp D, Saguez R, Decocq G (2010) Differential growth patterns and fitness may explain contrasted performances of the invasive *Prunus serotina* in its exotic range. Biol Invasions. doi:10.1007/s10530-010-9893-6

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Conway WC, Smith LM, Bergan JF (2002) Potential allelopathic interference by the exotic Chinese tallow tree (*Sapium sebiferum*). Am Midl Nat 148:43–53

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dezzotti A, Sbrancia R, Mortoro A, Monte C (2009) Biological invasion of *Pinus ponderosa* and *Pinus contorta*: case study of a forest plantation in Northwestern Patagonia. Invest Agrar-Sist Rec F 18:181–191

Donnelly MJ, Walters LJ (2008) Water and boating activity as dispersal vectors for *Schinus terebinthifolius* (Brazilian pepper) seeds in freshwater and estuarine habitats. Estuar Coast 31:960–968

Donnelly MJ, Green DM, Walters LJ (2008) Allelopathic effects of fruits of the Brazilian pepper *Schinus terebinthifolius* on growth, leaf production and biomass of seedlings of the red mangrove *Rhizophora mangle* and the black mangrove *Avicennia germinans*. J Exp Mar Biol Ecol 357:149–156

Erfmeier A, Bruelheide H (2010) Invasibility or invasiveness? Effects of habitat, genotype, and their interaction on invasive *Rhododendron ponticum* populations. Biol Invasions 12:657–676

Feng Y, Wang J, Sang W (2007) Biomass allocation, morphology and photosynthesis of invasive and non-invasive exotic species grown at four irradiance levels. Acta Oecol 31:40–47

Franks SJ, Pratt PD, Dray FA, Simms EL (2008a) No evolution of increased competitive ability or decreased allocation to defense in *Melaleuca quinquenervia* since release from natural enemies. Biol Invasions 10:455–466

Franks SJ, Pratt PD, Dray FA, Simms EL (2008b) Selection on herbivory resistance and growth rate in an invasive plant. Am Nat 171:678–691

Gaertner M, Den Breeyen A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog Phys Geogr 33:319–338

Gates S (2002) Review of methodology of quantitative reviews using meta-analysis in ecology. J Anim Ecol 71:547–557

Green PT, Lake PS, O'Dowd DJ (2004) Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance. Biol Invasions 6:1–9

Grotkopp E, Rejmánek M, Rost TL (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. Am Nat 159:396–419

Gurevitch J, Curtis PS, Jones MH (2001) Meta-analysis in ecology. Adv Ecol Res 32:199–247

Gurevitch J, Howard TG, Ashton IW, Leger EA, Howe KM, Woo E, Lerdau M (2008) Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biol Invasions 10:821–831

Hedges LV, Olkin I (1985) Statistical methods for meta-analysis. Academic Press, San Diego, CA

Heimpel GE, Frelich LE, Landis DA, Hopper KR, Hoelmer KA, Sezen Z, Asplen MK, Wu KM (2010) European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. Biol Invasions 12:2913–2931

Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. J Ecol 93:5–15

Higgins SI, Richardson DM (1998) Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecol 135: 79–93

Higgins SI, Richardson DM, Cowling RM (1996) Modeling invasive plant spread: the role of plant-environment interactions and model structure. Ecology 77:2043–2054

Hoffmann WA, Poorter H (2002) Avoiding bias in calculations of relative growth rate. Ann Bot-Lond 90:37–42

Howard TG, Gurevitch J, Hyatt L, Carreiro M, Lerdau M (2004) Forest invasibility in communities in southeastern New York. Biol Invasions 6:393–410

Huang W, Siemann E, Wheeler GS, Zou JW, Carrillo J, Ding JQ (2010) Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. J Ecol 98:1157–1167

Inderjit (2005) Plant invasions: habitat invasibility and dominance of invasive plant species. Plant Soil 277:1–5

Iponga DM, Milton SJ, Richardson DM (2009a) Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Anacardiaceae) in South Africa. Austral Ecol 34:678–687

Iponga DM, Milton SJ, Richardson DM (2009b) Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna. Biol Invasions 11:159–169

Iponga DM, Milton SJ, Richardson DM (2010) Performance of seedlings of the invasive alien tree *Schinus molle* L. under indigenous and alien host trees in semi-arid savanna. Afr J Ecol 48:155–158

Jackson RB, Banner JL, Jobbagy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626

Jones RB (1998) TechDig. Version 2.0d. Mundelein, IL

Kaproth MA, McGraw JB (2008) Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. Forest Sci 54:490–496

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Keay J, Rogers WE, Lankau R, Siemann E (2000) The role of allelopathy in the invasion of the Chinese tallow tree (*Sapium sebiferum*). Tex J Sci 52:57–64

Knapp LB, Fownes JH, Harrington RA (2008) Variable effects of large mammal herbivory on three non-native versus three native woody plants. Forest Ecol Manag 255:92–98

Knight KS, Reich PB (2005) Opposite relationships between invasibility and native species richness at patch versus landscape scales. Oikos 109:81–88

Knight KS, Oleksyn J, Jagodzinski AM, Reich PB, Kasprowicz M (2008) Overstorey tree species regulate colonization by native and exotic plants: a source of positive relationships between understorey diversity and invasibility. Divers Distrib 14:666–675

Krivanek M, Pysek P (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). Divers Distrib 12:319–327

Krivanek M, Pysek P, Jarosik V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. Conserv Biol 20:1487–1498

Kuppinger DM, Jenkins MA, White PS (2010) Predicting the post-fire establishment and persistence of an invasive tree species across a complex landscape. Biol Invasions 12: 3473–3484

Lankau RA, Rogers WE, Siemann E (2004) Constraints on the utilisation of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. Ecol Entomol 29:66–75

Leger EA, Howe KM, Gurevitch J, Woo E, Hickman J, Ashton IW, Lerdau M (2007) The interaction between soil nutrients and leaf loss during early 14 establishment in plant invasion. Forest Sci 53:701–709

Leimu R, Mutikainen P, Koricheva J, Fisher M (2006) How general are positive relationships between plant population size, fitness and genetic variation? J Ecol 94:942–952

Lesica P, DeLuca TH (2004) Is tamarisk allelopathic? Plant Soil 267:357–365

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Liu H, Stiling P (2006) Testing the enemy release hypothesis: a review and meta-analysis. Biol Invasions 8:1535–1545

Liu H, Stiling P, Pemberton RW (2007) Does enemy release matter for invasive plants? Evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners. Biol Invasions 9:773–781

Lockhart C, Austin DF, Aumen NG (1999) Water level effects on growth of *Melaleuca* seedlings from Lake Okeechobee (Florida, USA) littoral zone. Environ Manag 23:507–518

Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Divers Distrib 15:904–910

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536

Lorenzo P, Pazos-Malvido E, Gonzalez L, Reigosa MJ (2008) Allelopathic interference of invasive *Acacia dealbata*: physiological effects. Allelopath J 22:453–462

Lorenzo P, Pazos-Malvido E, Reigosa MJ, Gonzalez L (2010a) Differential responses to allelopathic compounds released by the invasive *Acacia dealbata* link (Mimosaceae) indicate stimulation of its own seed. Aust J Bot 58:546–553

Lorenzo P, Rodriguez-Echeverria S, Gonzalez L, Freitas H (2010b) Effect of invasive *Acacia dealbata* link on soil microorganisms as determined by PCR-DGGE. Appl Soil Ecol 44:245–251

Mack RN (1996) Predicting the identity and fate of plant invaders: emergent and emerging approaches. Biol Conserv 78:107–121

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373

Martin PH, Canham CD (2010) Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects. Oikos 119:807–824

Martin PH, Marks PL (2006) Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). J Ecol 94:1070–1079

Mazia CN, Chaneton EJ, Ghersa CM, Leon RJC (2001) Limits to tree species invasion in pampean grassland and forest plant communities. Oecologia 128:594–602

Mazia C, Chaneton EJ, Machera M, Uchitel A, Feler MV, Ghersa CM (2010) Antagonistic effects of large- and small-scale disturbances on exotic tree invasion in a native tussock grassland relict. Biol Invasions 12:3109–3122

McCay TS, McCay DH (2009) Processes regulating the invasion of European buckthorn (*Rhamnus cathartica*) in three habitats of the northeastern United States. Biol Invasions 11:1835–1844

Milbau A, Nijs I, Van Peer L, Reheul D, De Cauwer B (2003) Disentangling invasiveness and invasibility during invasion in synthesized grassland communities. New Phytol 159:657–667

Milton SJ, Wilson JRU, Richardson DM, Seymour CL, Dean WRJ, Iponga DM, Proches S (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. J Ecol 95:648–661

Morgan EC, Overholt WA (2005) Potential allelopathic effects of Brazilian pepper (*Schinus terebinthifolius* Raddi, Anacardiaceae) aqueous extract on germination and growth of selected Florida native plants. J Torrey Bot Soc 132:11–15

Morrison JA, Mauck K (2007) Experimental field comparison of native and non-native maple seedlings: natural enemies, ecophysiology, growth and survival. J Ecol 95: 1036–1049

Nasir H, Iqbal Z, Hiradate S, Fujii Y (2005) Allelopathic potential of *Robinia pseudo-acacia* L. J Chem Ecol 31:2179–2192

Nijjer S, Rogers WE, Siemann E (2007) Negative plant-soil feedbacks may limit persistence of an invasive tree due to rapid accumulation of soil pathogens. Proc R Soc B-Biol Sci 274:2621–2627

Nunez MA, Relva MA, Simberloff D (2008) Enemy release or invasional meltdown? Deer preference for exotic and native trees on Isla Victoria, Argentina. Austral Ecol 33:317–323

Ohlemüller R, Walker S, Wilson JB (2006) Local vs regional factors as determinants of the invasibility of indigenous forest fragments by alien plant species. Oikos 112:493–501

Peperkorn R, Werner C, Beyschlag W (2005) Phenotypic plasticity of an invasive acacia versus two native Mediterranean species. Funct Plant Biol 32:933–944

Pysek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W (ed) Biological invasions. Springer, Berlin, pp 97–125

Pysek P, Richardson DM, Rejmanek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143

Pysek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

Pysek P, Krivanek M, Jarosik V (2009) Planting intensity, residence time, and species traits determine invasion success of alien woody species. Ecology 90:2734–2744

Randall JM (1993) Exotic weeds in North American and Hawaiian natural areas: the nature conservancy's plan of attack. In: McKnight B (ed) Biological pollution: the control and impact of invasive exotic species. Indiana Academy of Sciences, Indianapolis, pp. 159–172

Randall JM (1996) Weed control for the preservation of biological diversity. Weed Technol 10:370–383

Reich PB, Peterson DW, Wedin DA, Wrage K (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. Ecology 82:1703–1719

Reinhart KO, Callaway RM (2004) Soil biota facilitate exotic *Acer* invasions in Europe and North America. Ecol Appl 14:1737–1745

Reinhart KO, Packer A, Van der Putten WH, Clay K (2003) Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. Ecol Lett 6:1046–1050

Reinhart KO, Greene E, Callaway RM (2005) Effects of *Acer platanoides* invasion on understory plant communities and tree regeneration in the northern Rocky Mountains. Ecography 28:573–582

Reinhart KO, Maestre FT, Callaway RM (2006) Facilitation and inhibition of seedlings of an invasive tree (*Acer platanoides*) by different tree species in a mountain ecosystem. Biol Invasions 8:231–240

Reinhart KO, Tytgat T, Van der Putten WH, Clay K (2010) Virulence of soil-borne pathogens and invasion by *Prunus serotina*. New Phytol 186:484–495

Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. Biol Conserv 78:171–181

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Rejmánek M, Richardson DM, Pysek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (ed) Vegetation ecology. Blackwell, Oxford, pp 332–355

Relva MA, Nunez MA, Simberloff D (2010) Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol Invasions 12:303–311

Reynolds LV, Cooper DJ (2010) Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US. J Veg Sci 21:733–743

Richardson DM (1998) Forestry trees as invasive aliens. Conserv Biol 12:18–26

Richardson DM (2006) Pinus: a model group for unlocking the secrets of alien plant invasions? Preslia 78:375–388

Richardson DM, Bond WJ (1991) Determinants of plant-distribution—evidence from pine invasions. Am Nat 137: 639–668

Richardson DM, Higgins SI (1998) Pines as invaders in the Southern Hemisphere. In: Richardson DM (ed) Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, pp 450–473

Richardson DM, Pysek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Prog Phys Geogr 30:409–431

Richardson DM, van Wilgen BW (2004) Invasive alien plants in South Africa: how well do we understand the ecological impacts? S Afr J Sci 100:45–52

Richardson DM, Williams PA, Hobbs RJ (1994) Pine invasions in the Southern-Hemisphere—determinants of spread and invasibility. J Biogeogr 21:511–527

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107

Richardson DM, Pysek P, Carlton JT (2011) A compendium of essential essential concepts and terminology in invasion ecology. In: Richardson DM (ed) Fifty years of invasion ecology. The legacy of Charles Elton. Wiley-Blackwell, Oxford, pp 409–420

Richardson DM, Rejmanek M. Trees and shrubs as invasive alien species—a global review. Divers Distrib (in press)

Rogers WE, Siemann E (2002) Effects of simulated herbivory and resource availability on native and invasive exotic tree seedlings. Basic Appl Ecol 3:297–307

Rogers WE, Siemann E (2003) Effects of simulated herbivory and resources on Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasion of native coastal prairie. Am J Bot 90:243–249

Rogers WE, Siemann E (2004) Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. J Appl Ecol 41:561–570

Rogers WE, Siemann E (2005) Herbivory tolerance and compensatory differences in native and invasive ecotypes of Chinese tallow tree (*Sapium sebiferum*). Plant Ecol 181:57–68

Rosenberg MS (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. Evolution 59:464–468

Rosenberg MS, Adams DC, Gurevitch J (2000) MetaWin: statistical software for meta-analysis. Sinauer Associates, Sunderland

Rouget M, Richardson DM (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. Am Nat 162:713–724

Rouget M, Richardson DM, Milton SJ, Polakow D (2001) Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecol 152:79–92

Saccone P, Pages JP, Girel J, Brun JJ, Michalet R (2010) Acer negundo invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. New Phytol 187:831–842

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Schumacher E, Kueffer C, Tobler M, Gmur V, Edwards PJ, Dietz H (2008) Influence of drought and shade on seedling growth of native and invasive trees in the Seychelles. Biotropica 40:543–549

Schumacher E, Kueffer C, Edwards PJ, Dietz H (2009) Influence of light and nutrient conditions on seedling growth of native and invasive trees in the Seychelles. Biol Invasions 11:1941–1954

Siemann E, Rogers WE (2001) Genetic differences in growth of an invasive tree species. Ecol Lett 4:514–518

Siemann E, Rogers WE (2003a) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. J Ecol 91:923–931

Siemann E, Rogers WE (2003b) Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84:1489–1505

Siemann E, Rogers WE (2003c) Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecol Appl 13:1503–1507

Siemann E, Rogers WE (2003d) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. Oecologia 135:451–457

Siemann E, Rogers WE (2006) Recruitment limitation, seedling performance and persistence of exotic tree monocultures. Biol Invasions 8:979–991

Siemann E, Rogers WE (2007) The role of soil resources in an exotic tree invasion in Texas coastal prairie. J Ecol 95:689–697

Siemann E, Rogers WE, Dewalt SJ (2006) Rapid adaptation of insect herbivores to an invasive plant. Proc R Soc B-Biol Sci 273:2763–2769

Siemann E, Rogers WE, Grace JB (2007) Effects of nutrient loading and extreme rainfall events on coastal tallgrass prairies: invasion intensity, vegetation responses, and carbon and nitrogen distribution. Glob Change Biol 13:2184–2192

Simberloff D, Nunez MA, Ledgard NJ, Pauchard A, Richardson DM, Sarasola M, Van Wilgen BW, Zalba SM, Zenni RD, Bustamante R, Pena E, Ziller SR (2010) Spread and impact of introduced conifers in South America: lessons from other southern hemisphere regions. Austral Ecol 35:489–504

Swanborough P, Westoby M (1996) Seedling relative growth rate and its components in relation to seed size: phylogenetically independent contrasts. Funct Ecol 10:176–184

Tecco PA, Gurvich DE, Diaz S, Perez-Harguindeguy NP, Cabido M (2006) Positive interaction between invasive plants: the influence of *Pyracantha angustifolia* on the recruitment of native and exotic woody species. Austral Ecol 31:293–300

Tecco PA, Diaz S, Gurvich DE, Perez-Harguindeguy N, Cabido M, Bertone GA (2007) Facilitation and interference underlying the association between the woody invaders *Pyracantha angustifolia* and *Ligustrum lucidum*. Appl Veg Sci 10:211–218

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol Lett 13:235–245

Vanhellemont M, Verheyen K, De Keersmaeker L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biol Invasions 11:1451–1462

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton

Williams JL, Auge H, Maron JL (2008) Different gardens, different results: native and introduced populations exhibit contrasting phenotypes across common gardens. Oecologia 157:239–248

Williamson M (1996) Biological invasions. Chapman & Hall, London

Williamson M (2006) Explaining and predicting the success of invading species. Biol Invasions 8:1561–1568

Williamson M, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666

Yamashita N, Koike N, Ishida A (2002) Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. Plant Cell Environ 25:1341–1356

Yelenik SG, Stock WD, Richardson DM (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. Restor Ecol 12:44–51

Zalba SM, Cuevas YA, Boo RM (2008) Invasion of *Pinus halepensis* Mill. following a wildfire in an Argentine grassland nature reserve. J Environ Manag 88:539–546

Zou JW, Rogers WE, DeWalt SJ, Siemann E (2006) The effect of Chinese tallow tree (*Sapium sebiferum*) ecotype on soil-plant system carbon and nitrogen processes. Oecologia 150:272–281

Zou JW, Rogers WE, Siemann E (2008a) Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. Biol Invasions 10:291–302

Zou JW, Siemann E, Rogers WE, DeWalt SJ (2008b) Decreased resistance and increased tolerance to native herbivores of the invasive plant *Sapium sebiferum*. Ecography 31:663–671

Zou JW, Rogers WE, Siemann E (2009) Plasticity of *Sapium sebiferum* seedling growth to light and water resources: inter- and intraspecific comparisons. Basic Appl Ecol 10:79–88