



## A meta-analysis of the ecological significance of density in tree invasions

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**Abstract:** Species richness, resource availability, and disturbance are the primary factors considered in assessing the invasibility of plant communities. Nonetheless, the density of individuals in a community is a common and easy trait to measure. The ecological significance of the density of both native and invasive tree species was assessed using a systematic review and formal meta-analysis. The densities of recipient communities and invasive exotic tree species in novel ranges were identified in the published literature. In addition, we compared by means of a meta-analysis: (i) densities of invasive *versus* native species in invaded communities; (ii) densities of native species in invaded *versus* uninvaded communities; and (iii) densities of invasive species along distance gradients from initial locus of invasion. Invasive trees were found at higher densities than native species in recipient communities. Invasions by woody species were also recorded in communities with relatively low densities of natives suggesting that (i) low density forests may be more susceptible to invasion and/or (ii) density of the recipient community may be reduced during the invasion process. In addition, comparison of native species densities between invaded and uninvaded stands from the same community suggests that invasive trees negatively affect density of native trees once established. Therefore, the widely reported low density and often richness of native plants in invaded communities cannot be directly linked to ecosystem susceptibility to invasion without considering concomitant impacts. These findings suggest that density is a key preliminary determinant or factor which should be considered when assessing tree invasion dynamics.

### Introduction

Invasive plants have major impacts on communities and ecosystems (D'Antonio and Vitousek 1992, Vitousek et al. 1996, Chapin et al. 2000, Mack et al. 2000), yet invasion by non-woody species is more widely studied than invasive exotic trees. This is unfortunate since trees are 'ecosystem engineers' driving resources availability, changing abiotic and biotic characteristics of an ecosystem and shaping the structure of entire landscapes (Jones et al. 1994). Moreover, the establishment from propagules to reproduction takes years, and thus, invasion by woody species is a much slower process which means that we could be facing a sleeping giant in terms of future impacts (Kowarik 1995). However, the long persistence of trees at various life-stages does offer a unique opportunity to explore whether density is an important measure of invasibility.

To date, invasibility of communities is commonly assessed using species richness (Elton 1958, Shea and Chesson 2002, Tilman 2004), and there are numerous examples demonstrating that species-rich communities are less easily invaded (Rejmanek 1989, Knops et al. 1999, Kennedy et al. 2002, Levine 2000). Species richness cannot of course single

handily explain community invasibility and requires the consideration of factors such as disturbance, climate, and resource availability (Levine and D'Antonio 1999, Kneitel and Perrault 2006). Fluctuating resources (Davis et al. 2000, Colautti et al. 2006) and empty niches (Levine and D'Antonio 1999) have also been invoked to explain why communities vary in the extent that they are invaded. Nonetheless, these theories of plant invasions were developed almost exclusively in grasslands (Levine et al. 2004, Martin et al. 2008). We propose that the density of the recipient community (number of individuals per unit area sampled) is an intuitive variable to measure in many systems for all these theories. Density often co-varies with richness (Levine et al. 2004) and could be a surrogate for both resource availability and available space. More specifically, density ranges of recipient communities may provide the means to assess the types of communities most susceptible to invasion. We thus propose that density can be a key factor related to ecosystem invasibility since introduced individuals can be controlled to some extent by the broad factor of the recipient community density (Davis et al. 2000) via the mechanisms proposed in the larger theories of invasibility such as resident competitor contribution to biotic resistance (Levine et al. 2004), empty niche

(Levine and D'Antonio 1999) or fluctuating resources (Davis et al. 2000).

Including environmental and ecological impacts of exotics on recipient communities in the definition of invasive species is still debated (Valéry et al. 2008) since measurement of impacts is difficult. Therefore, recent studies have focused on exotic tree impacts on recipient communities using changes in community diversity via exclusion of natives (e.g. Fang 2005), changes in the associated understorey diversity (e.g. Avalos et al. 2006), or changes in forest functions (e.g. Gómez-Aparicio et al. 2008; Martin et al. 2009). Mason and French (2008) suggested that the impact of an exotic woody species in natural systems is dependent on characteristics of the invaded community (vegetation structural density, richness of both native and exotic growth forms and community variability). However, exotic species do not automatically pose a threat to native biota (Goodenough 2010) and little is known about the impact of invasive trees on the density of native species from the recipient community. Comparing the density of native species for invaded and non-invaded patches from the same community in the novel range provides a relevant assessment of the impact of the invasive tree since more invaders should at some level at least lead to less native trees (e.g. Gareca et al. 2007).

Given the increasing rate of invasion of exotic plants and the potential for density measurements of native and invasive species to explain invasion patterns, an enhanced understanding of the general trends associated with density and invasion by trees will not only increase the scope of generality of the theories explaining invasion, but further our capacity to predict and manage invasion in forests. As the number of studies published on this topic increases, synthetic treatment can help assess whether trends across studies are emerging and help refine studies of particular processes (Adams et al. 1997). Although narrative reviews are useful as summaries of the knowledge within a discipline, a quantitative and direct comparison of effect sizes between studies via meta-analysis provides the means to assess the evidence for a particular hypothesis (Gates 2002). Our primary purpose is thus to test the conceptual viability of density in understanding invasibility and impacts both of which are often blended and tested in various ways using the more specific hypotheses associated with the invasion literature. We used a comprehensive review of the literature to identify the density ranges of recipient communities and invasive exotic tree species in novel ranges and a formal meta-analysis to compare densities of invasive *versus* native species in invaded communities; densities of native species in invaded *versus* uninvaded stands from the same community; and densities of invasive species along distance of study site from initial locus of invasion. Specifically, we addressed the following questions: (1) Are papers studying biological invasion always focused on species clearly defined as invasive, i.e. with a high density relative to native species in the recipient community or is the definition based on impact? (2) Do invaded communities have low density of native species? (3) Is the density of native species lower in invaded than in non-invaded patches

from the same community? (4) Are densities measured along the colonization front relevant to infer extent of invasion?

## Methods

### Data collection

To explore the density ranges in studies testing invasion in trees, we conducted an extensive survey of the literature using a combination of 'densit\*', 'tree' and 'invas\*' as keywords in the electronic database ISI Web of Science. This search led to a large number of papers that were subsequently examined for their suitability in our review and meta-analysis. Inclusion criteria included explicit address of tree ecology using an exotic woody invasive species, and reporting of a definitive measure of density in novel ranges. Using these criteria, articles on proliferation of native woody species (i.e. succession studies or establishment of native trees in old fields) were excluded.

In this set of papers, densities (number of individuals per unit area, including means, maxima and minima) were recorded for each invasive woody species in novel ranges when provided whatever the aim of the study, and were categorized according to the different stages in the life cycle of species: adult trees, seedlings (including seedlings, saplings and juveniles) and seeds (including seeds and germinants). Densities of recipient communities (overall number of trees per unit area) were obtained either by summing the density of each species from the community or with the density of the most representative native species in the community as indicated by authors (namely that other species were rare relative to this particular species). For each study, we recorded when provided, sample sizes (i.e. number of plots used to assess native or invasive species density), standard errors, and the numerical density data. When values were not reported, data from graphs were scanned and extracted in table format using TechDig software (Jones 1998).

In addition, for each study we recorded whether it was observational or experimental. We classified studied areas as temperate (from latitude 35° to 50°) or tropical (from latitude 10° to 35°) using the reported latitudes or as notified in manuscripts. Invasive woody species were also categorized as deciduous or evergreen.

### Meta-analytical methods

A set of criteria were defined *a priori* for inclusion in the quantitative meta-analyses. Studies must have reported sample sizes (number of plots used to assess density), standard errors, and the numerical density data. We selected Hedge's unbiased standardized mean difference ( $d$ ) as the metric of effect size for this meta-analysis (Gurevitch and Hedges 2001) because it accounts for the large variations in sample sizes present in data sets (Hedges and Olkin 1985). We calculated  $d$ , its associated 'Var ( $d$ )', and conducted the meta-analysis using the program Metawin 2.0 (Rosenberg et al. 2000). This effect size metric measures the effect of study-

**Table 1.** Details for calculation of effect size metrics (Hedges'  $d$ ) according to three density categories. For each one, the response variable means from experimental vs. control groups were performed. Densities are numbers of individuals per species per unit area. Abbreviations of the three density categories used in the meta-analysis are shown in parenthesis.

Comparisons	Experimental group	Control group
Density of the natives <i>versus</i> invasives in novel ranges ( <i>Nat vs. Inv</i> )	Density of invasive trees from an invaded stand	Density of native communities from an invaded stand
Density of natives in invaded <i>versus</i> uninvaded stands from the same community in the novel range ( <i>Nat</i> )	Density of native communities from a non-invaded stand	Density of native communities from an invaded stand
Densities of invasive trees in novel ranges along colonization front ( <i>Inv</i> )	Density of invasive trees closed to the invasion origin	Density of invasive trees far from the invasion origin

specific experimental values on control values. Various comparative differences were calculated as presented in Table 1. To obtain experimental and control mean densities, data points from scatter plots and correlations were treated in several ways depending on the vagaries of the particular study. The lowest *versus* highest values (mean and standard deviation) of the independent variable were used, or the mean value and standard deviation was calculated by pooling the data points for the higher-half values (used as control values) and lower-half (used as experimental values) of the continuous independent variable. We interpreted  $d$  as an indicator of the ecological significance of density measurements in tree invasions. If the individual or pooled effect sizes were significantly different from zero, the density measurement was treated as an effective index of likelihood of invasion by woody species.

We included studies that compared (i) densities of invasive trees *versus* native communities in invaded stands in novel ranges; (ii) densities of native communities in invaded *versus* uninvaded stands from the same community in the novel range; and (iii) densities of invasive species along distance transects from invasion origin (colonization front) (Table 1). When a single study presented results for multiple species, we considered each species as an independent data record (Aguilar et al. 2006). In the same vein, when a study used different life stages to measure the density of a species (i.e. seed density and seedling density), we considered each type of measurement as an independent data record. However, sensitivity analyses via exclusion of multiple entries per study were done to ensure that the trends detected are general and not a product of several larger studies (Lortie and Callaway 2006). Finally, where species were studied in multiple locations in a single publication, one location was randomly selected for inclusion in the meta-analyses to reduce geographical bias. In the event that density was recorded at various time intervals, we decided to consistently work only with the data taken for the most mature life-stage.

Tests for significant differences between densities and 95% confidence intervals of effect sizes were done with MetaWin 2.0 (Rosenberg et al. 2000). Confidence interval (CI) of effect sizes were calculated using bootstrap resampling procedures (9999 iterations) as described in Adams et al. (1997). An effect size was considered significant if the 95% biased-

corrected bootstrap CI of the effect size ( $d$ ) did not overlap zero (Rosenberg 2000). Data were analysed using random-effect models (Raudenbush 1994). Random effect models are preferable in ecological data synthesis and their assumptions are more likely to be satisfied (Gurevitch and Hedges 2001).

Q-statistics were used to examine the heterogeneity of effect sizes (Hedges and Olkin 1985). The variance (Q) among effect sizes is tested via randomization to determine if it is significantly different from chance or randomness (Cooper 1998), and a categorical comparison of the Q associated with three categories of density (see Table 1) was performed. A categorical analysis was also performed on pooled data to test whether density has the same ecological significance under a temperate or a tropical climate.

Publication biases were tested statistically with a Spearman rank correlation test and a weighted fail-safe number. If the fail-safe number is larger than  $5n + 10$  (where  $n$  is the number of studies) then publication bias is not present in the selection of studies (Rosenthal 1991, Rosenberg 2005).

## Results

### *Systematic review of the literature*

A total of 147 articles included the terms 'densit\*', 'tree' and 'invas\*' were recorded and the final data set appropriate for analysis included 25 studies in 18 different journals from 1995 to 2008 (see Appendix A in Supplementary Material). Within this set of publications, 56% dealt with the impact of invasive tree species on recipient communities, 28% with spatial pattern of invasion, and 16% with invasive seed ecology. All studies were conducted in invaded habitats *in situ*. Three publications were manipulative (by planting or removing invasive trees), and 22 were observational.

Invasive trees in recipient communities presented a large range of density for all the life stages observed (e.g. from 4.61 to 8 845 adult trees per hectare) (Table 2). These studies generally recorded densities from 100 to 1000 stems per hectare at the 'adult' life stage (56%) and 87.5% of species were recorded with densities higher than 100 stems per hectare (Fig. 1). However, some studies used the term invasive for tree species exhibiting less than 100 stems per hectare (Table

**Table 2.** The mean reported densities for invasive tree species in novel ranges from a systematic review of the literature, according to the different stages in the life cycle of tree: adults, seedlings, and seeds. Mean values correspond to the number of individuals per species and unit area.

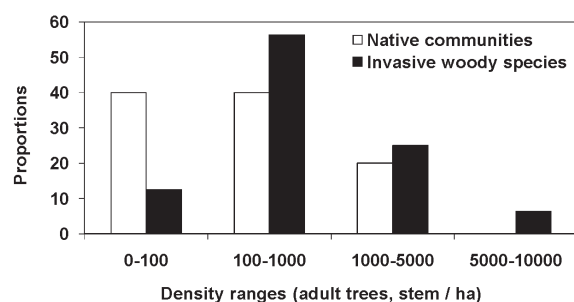
	Minimum density			Maximum density		
	Species	Mean values stem/ha *or seed/m <sup>2</sup>	Region and Source	Species	Mean values stem/ha *or seed/m <sup>2</sup>	Region and Source
Adult trees	<i>Acer Platanoides</i> Aceraceae	4.61	Temperate forest island (US)	<i>Pseudotsuga menziesii</i> Pinaceae	8845	Montane mediterranean forests (Spain)
Seedlings	<i>Picea abies</i> Pinaceae	280	Temperate grassland (Slovakia)	<i>Acer platanoides</i> Aceraceae	10 <sup>6</sup>	Forest (US)
Seeds	<i>Ailanthus Altissima</i> Simaroubaceae	0.4*	Mixed habitat in Virginia (US)	<i>Acacia saligna</i> Fabaceae	2067*	Fynbos vegetation (South Africa)

**Table 3.** A summary of the categorical analyses used in a meta-analysis. Hedge's *d* is an estimate of effect size with 0 being no relative effect of density. Q-statistics are an estimate of variability estimated between the groups of treatments. Abbreviations are: bias confidence interval (CI), Nat vs. Inv, Nat and Inv correspond to categories presented in Table 1, temperate climate (TE), tropical climate (TR). See text for full details.

Analysis	Effect size Hedges' <i>d</i>	Q statistics
Overall weighted-mean effect size	$d = 1.21$ (CI 0.71 to 1.84)	$Q_{\text{between}} = 17.6$ $n = 21, P = 0.6$
Density categorical analysis	$d_{\text{Nat vs. Inv}} = 1.45$ (CI 1.09 to 2.07) $d_{\text{Nat}} = 1.64$ (CI 0.59 to 3.07) $d_{\text{Inv}} = 0.62$ (CI -0.1 to 1.16)	$Q_{\text{between}} = 2.53$ $n = 3, P = 0.34$
Climate categorical analysis	$d_{\text{TE}} = 1.11$ (CI 0.49 to 1.95) $d_{\text{TR}} = 1.68$ (CI 1.23 to 2.36)	$Q_{\text{between}} = 0.48$ $n = 2, P = 0.45$

2, Fig.1). In addition, recipient communities were more frequently reported in the two lowest density ranges (80% of studies ranged from 0-100 and 100-1000 stems per hectare, Fig. 1).

The life stage most commonly recorded was the 'seedling' stage representing 46% versus 39% of studies recording adult tree densities and 15% recording seed densities. There were 21 invasive tree species (71% deciduous species, 29% evergreen) studied in twelve families (29% belonging to the Pinaceae family) in thirteen different countries (Fig. 2). Four studies evaluated more than one invasive tree species simultaneously (Drake 1998; Hughes and Denslow 2005, Avalos et al. 2006, Gareca et al. 2007). In this set of studies, 76%



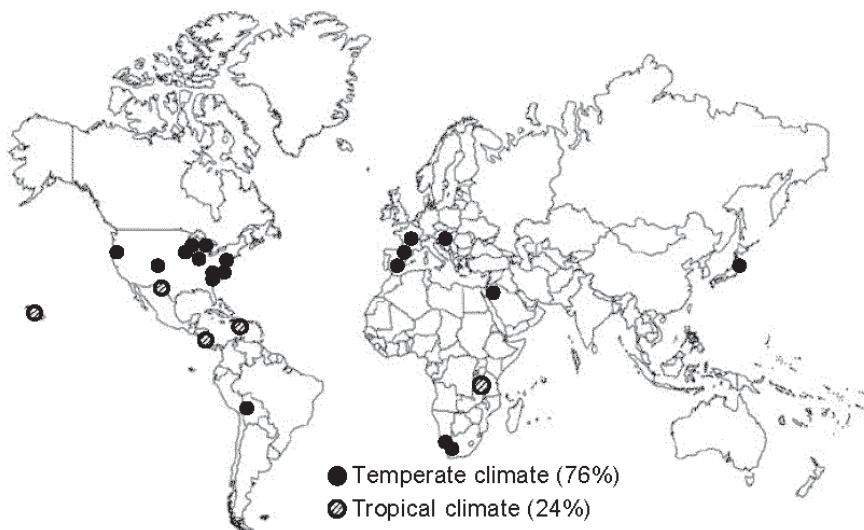
**Figure 1.** Extent of native/exotic representation in recipient communities as estimated by the proportion of adult tree species within each density class ( $n = 5$  for native communities and  $n = 16$  for invasive tree species). See text for inclusion criteria.

were done in a temperate climate, 24% in a tropical climate, and 64% of the tree invasion studies were done in forests, the others in grasslands, dunes or riparian habitats.

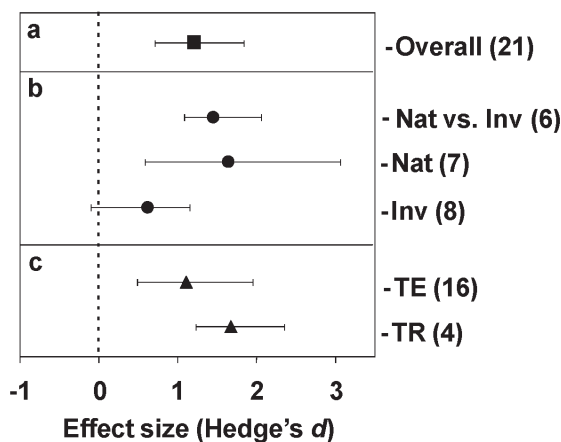
#### Meta-analytic trends

Fifteen studies were amenable to meta-analysis (fourteen included in the systematic review and an additional study carried out under control conditions; see Appendices A and B in Supplementary Material). We calculated 21 effect size estimates from these studies for 15 different invasive tree species. There was no evidence of publication bias in the studies included in this meta-analysis (Spearman rank order correlation of effect sizes vs. sample size,  $R_s = 0.151$ ,  $p = 0.51$ ). Finally, the calculated fail-safe number (1179.2) was much greater than expected (115) without publication bias. The overall heterogeneity of effect sizes was not statistically significant indicating that the studies were appropriately grouped ( $Q_{\text{total}} = 17.6$ ,  $n = 21$ ,  $P = 0.6$ ). The grand mean across the 21 studies was positive ( $d = 1.21$ ) and significantly different from no effect (Fig. 3a, Table 3) indicating the ecological significance of density comparisons in patterns of tree invasions.

Since not all studies evaluated all classes of comparisons (see Appendix B in Supplementary Material), sample size varied among analyses. Five studies recorded only density of the natives *versus* invasives in novel ranges (Nat vs. Inv), 6 recorded only density of natives in invaded *versus* uninvaded stands in the novel range (Nat) and 5 recorded densities of invasive trees along distance transects in novel ranges (Inv).



**Figure 2.** The geographic locations and climates of tree invasion studies included in the systematic review ( $n = 25$ ). See text for inclusion criteria.



**Figure 3.** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of density in tree invasion including the grand mean and each set of contrasts (see text for description). Whole sample of species (a), density categorical analysis (b) and climate categorical analysis (c). Sample sizes for each categorical grouping of the data are shown in parentheses; Abbreviations are: ‘Nat vs. Inv’, ‘Nat’, ‘Inv’ correspond to categories presented in Table 1, temperate climate (TE), tropical climate (TR). Effect sizes are significantly different from no effect if the 95% biased-corrected bootstrap CI of the effect size ( $d$ ) did not overlap zero.

First, invasive tree densities were significantly greater than native tree densities in invaded stands (Table 3 and Fig. 3b, *Nat vs. Inv*) and second, native tree densities were significantly lower in invaded stands than in non-invaded stands in the novel ranges (Table 3 and Fig. 3b, *Nat*). However, the effect size comparing densities of invasive trees by distance on transects was not significantly different from no effect (Table 3 and Fig. 3b, *Inv*). Furthermore, for each climate category, effect sizes were significantly different from no effect but they did not differ from each other ( $Q$  statistics, Table 3 and Fig. 3c), arguing for the significance of density meas-

urements in tree invasion both under temperate and tropical climates.

### Discussion

The systematic review and meta-analysis both supported the main hypothesis here that relative density in tree communities is strongly correlated with invasion and is also a potential indicator of some of the broader impacts associated invasion. While this is the first systematic review of density and invasion, it suggests that density can serve as a starting point in assessing invasibility and impacts thereof through a quick, preliminary measure of a community. However, density dependence is a common phenomenon in most plant functional groups (Berryman et al. 2002, Gunton and Kunin 2009, Lortie and Turkington 2002, White 2001), and several preliminary studies using invasive grassland species also suggest that density is a useful community-level tool in other ecosystems (Lortie et al. 2010, Lortie et al. 2009). We here evidenced that tree invasions are mostly found in forest communities with low density, partly because they significantly reduce the density of native species. When studying the determinant of invasibility (species richness, density studies and resource availability), the impact of invasive trees on native species in recipient communities should therefore be taken into account.

Firstly, density of both invasive and native species from the recipient community was ecologically relevant in modeling invasion since the effect sizes were significantly different from no effect and positive. Secondly, invasive trees were often found at densities higher than the natives in the recipient communities with the density of invasives mostly higher than 100 stems per hectare. Studies on biological invasion also focused on species that can be defined or categorized as invasive via relative density. Few studies classified exotic tree species as invasive when found at less than 100 stems per hectare which indicates that in studies involving trees the invader needs to achieve an appreciable density to warrant



study either because its negative effects are visible or because the local community is dramatically transformed (Vitousek 1990). Further identification of thresholds associated with invasive species will elucidate critical processes and provide valuable insights relevant to management since 100 stems per hectare may be arbitrary to some extent and it would be very useful to assess if other species not used in this review 'become' invasive at similar or lower densities.

The extent of invasion in forests using distance along colonization fronts was not an effective means to model invasion in these studies. The density effect varied among studies (effect sizes either positive or negative) and thus, no general trend could be assessed (non-significant effect size metric) to infer extent of invasion. This was not an unrealistically broad idea to explore in a meta-analysis since several studies have recorded a high density of invasives close to the invasion origin (e.g. Bruce et al. 1995) whilst other studies recorded the opposite trend explaining the low density of invasives near the invasion origin by a high competitive interaction for germination (Dovciack et al. 2008). Thus, density measures of invasives along distance gradients from initial locus of invasion can serve as a potential predictive/independent variable of invasion considering the ecological context of a particular study but not in a general manner.

Invasions by woody species were recorded in communities with low densities of natives. Two alternative but non exclusive hypotheses may explain this pattern. This trend could be explained by a greater invasibility of low dense area as they appeared possibly more sensitive to invasion (Elton 1958, Levine and D'Antonio 1999). A low density of natives in recipient communities signifies that little space is controlled by individuals and necessarily constitutes a set of resources available to introduced species, likely increasing the invasibility of these communities. More specifically, competitive interactions within recipient communities have been proposed as the process most directly contributing to biotic resistance (Levine et al. 2004) and might be used to predict where invasions are most likely to occur (Levine and D'Antonio 1999). Competition is likely to be more severe in high density communities than in sparse ones resulting in strong biotic resistance in the former and high sensitivity to invasion in the latter. In studies assessing competition effects on invasion, invasions were compared in intact communities to treatments in which resident competitors were removed (Levine et al. 2004 and references herein), using density of recipient communities to predict which communities are most susceptible to invasions. Other processes may contribute to biotic resistance: the species richness and niche availability (Levine and D'Antonio 1999, Shea and Chesson 2002) and the fluctuating resource availability hypothesis (Davis et al. 2000). The saturation hypothesis is often proposed to explain the sensitivity to invasion i.e. species rich areas have a lower invasibility than species poor areas (Tilman 2004). However, the empty niche hypothesis appears to be too restrictive to quantify the ecosystem invasibility in forests (Levine et al. 2004) and undisturbed plant communities are assumed to strongly resist exotic invasions (Martin et al. 2008). Density

of recipient communities and not only species richness and disturbance must be taken into account to accurately assess invasibility in forests.

However, the broad patterns in density detected here could be that lower native densities in invaded communities are a response and not a cause of invasion. Tree invasions can have negative long term impacts on natives that then lead to lower density ranges for the associated recipient communities. This is a form of negative feedback or 'melt-down' since increasing invader density propagates lower native densities likely due to interference. Herein, we found a positive effect size for the contrast of native densities in invaded and non-invaded stands from the same community, and this does suggest negative feedback since community was controlled. In each paper used in the present meta-analysis, the impact of invasive trees on recipient communities had been measured comparing similar non-invaded and invaded communities or by experimentally removing invasive trees. Native densities were similar before the invasion process and the effect size clearly suggests that density of natives is negatively impacted by invasion. Generally changes in density following removal or comparisons between invaded and non-invaded stands in single forests also support this interpretation (e.g. Hughes and Denslow 2005, Mason and French 2008, Webb et al. 2001). Low density communities that may be more sensitive to invasion suffer from the negative impact of the invasive species once invasion has occurred. This results in a further decrease in density of native species and may lead these species to a vortex of extinction. However, studies testing relationship between sensitivity to invasion (invasibility) and density *post hoc* (or in the same vein species richness) without controlling for the negative impact of invasive species are biases since they cannot disentangle both processes.

## Conclusions

This meta-analysis quantitatively demonstrated that density in tree communities is an important ecological consideration in relation to invasion. More specifically, native density in recipient community is related to the impact of the invasive tree species. Density as a concept and a measure is also a broad factor that integrates biotic factors like interference and abiotic factors such as resource availability, dispersal limitations, or available space (Guo and Symstad 2008). Consequently, while these factors are not addressed in this body of literature and hence meta-analysis, we recommend that measuring density in conjunction with any of these additional factors profoundly increases our ability to predict invasibility. To test for the effects of density on community invasion resistance independent of invasive species impact, we should experimentally examine to what extent variation in density of native species affected the establishment and success of the exotic species. Ironically, the designation of a species as invasive must at some level also rest upon recognition of changes in the relative density of these species with the most noxious of invaders being found at the highest densities within a community. Relative densities between natives and

exotics contrasted between native and novel ranges and within novel ranges can thus not only further more accurate definitions of invasion (Hiero et al. 2005) but also enhance our understanding of fundamental population and community-level dynamics. Moreover, most of the reviewed studies took place in North America (44%) and in Europe (16%). This explained the presence of a strong geographical bias, with Africa and especially Asia understudied, inhibiting a balanced understanding of invasion and demonstrated the importance of international cooperation to achieve a more geographically balanced picture of biological invasions (see also Pysek et al. 2008).

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## Appendices

*Appendix A.* Field studies that quantified tree invasions: data source, type of density measurements, invasive tree species, climates, tree strategies, habitat types, geographic regions, inclusion in meta-analysis, and effect sizes.

*Appendix B.* List of 15 studies included in the formal meta-analysis.

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