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Ecology and Evolution of Invasive Maple Tree Species

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Introduction

Context of the project

Biological invasions represent a major driver of the current human-induced decline of biodiversity worldwide (Chapin et al. 2000; Sala et al. 2000). Their effects are comparable to climate warming, land use changes and disturbances in general (Box 1). Ecological and socio-economical costs of invasive species have become increasingly apparent over time, and research in invasion biology has consequently expanded at an exponential rate in the last 30 years (Gurevitch et al. 2011). A huge literature now exists on population and community ecology and short-term evolution aspects of biological invasions (Bossdorf et al. 2005; van Kleunen et al. 2010; Felker-Quinn et al. 2013; Price and Pärtel 2013). More than two-dozen hypotheses have been proposed to explain the success of invaders in various contexts (Table 1), and there is now extensive evidence that one single explanation is not sufficient to describe all invasion processes (Hierro et al. 2005; Catford et al. 2009; Gurevitch et al. 2011). Invasion biology is thus a well-developed field of research which provides opportunities to better understand the role of introduction history, species functional traits, and ecological and evolutionary processes in shaping species coexistence and diversity as well as community organization.

Nonetheless, there are two major research gaps that are particularly relevant to this thesis: biogeographical contrasts and studies of invasive tree species. Demographic processes such as population increase, local dominance, and range expansion are central to invasion (Gurevitch et al. 2011), and invasive plants are assumed to occur at greater density and/or abundance at sites in their introduced (away) *vs.* native (home) range (Hierro et al. 2005; Williams et al. 2010). However, direct demographic comparisons between ranges remain scarce, and it is still unclear

Box 1: definition of biological invasions

Species called exotic (= alien, introduced) are those whose presence in a region is the result of a human-mediated transport, either accidentally or intentionally (Richardson and Pysek 2006). Exotic species represent to date a significant part of the vascular flora in many places around the globe: about half in Hawaii and New Zealand, 21% in Great Britain, 24% in Canada, 10-30% in mainlands of the USA, 12.5% in Europe and 10% in Australia (Vitousek et al. 1996). Naturalized species are exotics that succeed in forming self-replacing populations for at least 10 years via recruitment of seeds or vegetative propagation (Richardson and Pysek 2006) whereas invasive species are those producing reproductive offspring at significant distances of source plants and thus having the potential to spread over large areas (Elton 1958; Mack et al. 2000; Colautti and MacIsaac 2004). The process of invasion can be conceptualized as a series of separated barriers or stages that introduced species must overcome before becoming invasive (Fig. 1; Williamson and Fitter 1996; Richardson and Pysek 2006; Blackburn et al. 2011). It is often difficult to estimate the proportion of exotic species becoming invasive (Jeschke and Strayer 2005; Rodriguez-Cabal et al. 2013), but as a point of reference, it is usually noticed that 1 in 10 introduced species become naturalized and that 1 in 10 of those naturalized become invasive species (the ‘Tens Rule’; Williamson and Fitter 1996).

Invasive species are considered the second greatest cause of biodiversity loss after habitat destruction by human activities and a significant component of the global change affecting natural ecosystems for several decades (Vitousek et al. 1997; Lee 2002; Didham et al. 2005). Economic costs associated with invaders are also important because of major economic losses in agriculture, fisheries and forestry as well as expensive management actions (Dukes and Mooney 1999, Williamson 1999, Pimentel et al. 2000; Sakai et al. 2001; Pimentel et al. 2005). Biological invasions have consequently become a priority topic among ecologists, land managers and policy makers (D'Antonio and Kark 2002; Lodge et al. 2006).

if this scenario is common among exotic plant species (Hinz and Schwarzlaender 2004; Firn et al. 2011). Moreover, while common garden experiments are well suited to test the role of evolutionary changes in the success of invasive species (Siemann and Rogers 2001; Maron et al. 2004), most of them used only one common environment either in the native (Wolfe et al. 2004; Oduor et al. 2011; Wang et al. 2011) or the introduced range (Siemann and Rogers 2001; Caño et al. 2008; Kumschick et al. 2013). This can lead to serious pitfalls of data interpretation if plants finally respond differently to different growing conditions (Williams et al. 2008; Moloney et al. 2009). At this moment, only six studies properly tested the role of evolutionary changes in invasion success by setting up reciprocal common gardens in both native and introduced ranges (Table 2). Hence, although biogeographical approaches give the invasion biology research a larger scope of potential inferences in ecology and evolution, their paucity still undermines our understanding of determinants of invasiveness.

In addition, ecological and evolutionary processes involved in species invasions have been thoroughly studied only for a minority of invasive species (Pysek et al. 2008). This taxonomic bias is especially clear for invasive tree species. Out of the 357 tree species considered invasive to date (Richardson and Rejmanek 2011), invasion hypotheses have been tested on 114 of them (Table 3), but evolutionary changes via common garden experiments have solely been studied for two species, *Triadica sebifera* L. and *Melaleuca quinquenervia* (Cav.) Blake (Siemann and Rogers 2001; Franks et al. 2008). The lack of focus on invasive trees is detrimental because these species are ecosystem engineers, and their longer life span compared to herbaceous species can speak to the long-term dynamics and effects of invasions. Since no other invasive trees have previously been tested through reciprocal common gardens (Table 2), the biogeographical approach of this project provides a step forward into our understanding of the relative importance of environmental conditions, evolutionary changes and genotype-environment interactions that shape tree invasions.

Invasion success of *Acer negundo* L. and *Acer platanoides* L. (see Appendix 1 for a detailed description of both species) has also implications for the research in ecology and evolution in general. Two broad themes would particularly benefit from insights gained from the study of these two invasive tree species:

(*i*) habitat conservation and invasive species management. There is a growing need of models that could anticipate invasions (Mack et al. 2000; Wang et al. 2011). Niche-based and process-based models that have been developed in this way to predict the potential future range of invasive species require however a detailed understanding on species distribution, spread dynamics and species ecological tolerances (Peterson 2003; Wang et al. 2012). It is therefore crucial to detect key functional traits that would be determinants of species invasiveness, and specific environmental conditions under which exotic species would be more prone to proliferate (Moles et al. 2008; van Kleunen et al 2010; Hinz et al. 2012). These findings would also be valuable to improve management strategies that use trait-based and nitrogen immobilization approaches (Funk et al. 2008; Perry et al. 2010).

(*ii*) tree species adaptation to environmental changes. Forests are sensitive to climate change because the long life-span of trees does not allow them to rapidly adapt to environmental changes (Lindner et al. 2010). A major concern in ecology and evolution is thus the ability of tree species to respond to climate change that is occurring at an unprecedented rapid rate (Alberto et al. 2011). Tree populations can track climate change via phenotypic plasticity, evolutionary changes and genetic adaptation to new conditions, or via a combination of these responses (Aitken et al. 2008). Adaptation of exotic species to new environments can occur within a few decades after their introduction in new regions, *i.e.* quite rapidly compared to the timeline of plant evolution (Dlugosch and Parker 2008a), and invasive tree species hence represent good instances to study the short-term adaptive potential of tree populations to changing environmental conditions.

Invasion biology: an attractive and growing field of research

Hypotheses related to invasions

Biological invasions are complex processes. Numerous hypotheses referring to various mechanisms have been postulated and tested to explain the success of invasive species. Because most of them rely on similar predictions and overlap in mechanism, it is possible to structure them around three general drivers of invasion (Table 1, Fig. 2; Catford et al. 2009; Gurevitch et al. 2011):

(i) the propagule pressure, related to dispersal and geographical constraints. Successful invasion requires both sufficient number of individuals and/or seeds introduced and high frequency of introduction events (Lonsdale 1999; Foxcroft et al. 2004; Pysek and Richardson 2006). Propagule pressure is positively correlated to human population density and proximity (Pysek et al. 2010), and increases the chance that a species will adapt to novel conditions by enhancing genetic diversity of introduced populations (Lockwood et al. 2005). It may also explain the minimum lag period required before invasions occur, as the number of propagules introduced generally increases with time (Rejmanek 2000). Some authors thus consider this factor as the key driver of invasion.

(ii) the abiotic characteristics, linked to environmental and habitat constraints. Invasion cannot occur if a species does not survive or tolerate the conditions of the site it was introduced in. Moreover, several hypotheses attributing invasion to environmental factors are often based on a change in resource availability, via frequent or occasional anthropogenic or natural disturbances (Levine and D'Antonio 1999; Davis et al. 2000; Blumenthal 2006). Resource availability can fluctuate following an increase in resource supply or a reduction in resource uptake by native species. This refers to community invasibility, suggesting that more diverse communities may be less prone to invasion due to higher levels of biotic resistance and interspecific competition.

(iii) the biotic characteristics, referring to internal dynamics and population interactions. Enemy release, evolution of competitive ability, allelopathy and invasional meltdown are processes that can favour invasion whereas the loss of beneficial mutualistic relationships, biotic resistance and competition from dominant native species generally impede it (Callaway and Aschehoug 2000; Keane and

Crawley 2002; Levine et al. 2004). This category is therefore closely related to the functional traits conferring species invasiveness (see below).

Invasion occurs when there is an interaction between these three driving forces (Fig. 2). Habitats with high resource availability are for instance more susceptible to be invaded by exotic species possessing traits conferring fast growth such as high maximum assimilation rate and specific leaf area (Leishman et al. 2010). This explains why different individual hypotheses have been successfully tested on the same invasive species. Nutrient availability, allelopathic effects on native species and evolutionary shifts towards increased competitive ability and herbivory tolerance were all found to be important determinants of the invasion success of *Triadica sebifera* and *Centaurea spp*. in their introduced ranges (Keay et al. 2000; Vivanco et al. 2004; Siemann et al. 2007; Zou et al. 2008; He et al. 2009; Hierro et al. 2009; Andonian and Hierro 2011). Nonetheless, despite increasing knowledge on the mechanisms driving invasion, some areas need further attention. Propagule pressure should be quantified for more species and in different ecosystems, and this would improve the current frameworks developed to anticipate and prevent invasions in general. Moreover, abiotic and biotic drivers of invasion have mainly been tested independently from each other, and it is now necessary to assess the relative importance of community invasibility and species traits conferring invasiveness simultaneously, and on a larger array of invasive taxa.

Traits associated with species invasiveness

Predicting which species are more likely to become invasive has been a major goal in invasion biology. A common line of investigations has therefore been the search for the kinds of functional traits that could promote invasiveness. There has been significant work examining this via comparisons of traits between invasive and non-invasive species (Baruch and Goldstein 1999; Garcia-Serrano et al 2004; Xu et al. 2007; Osunkoya et al. 2010).

Several recent meta-analyses have tried to find general patterns across a wide range of ecosystems and species (Daehler 2003; Hawkes 2007; Pysek and Richardson 2007; van Kleunen et al. 2010; Firn et al. 2011; Ordonez et al. 2010). Invasive species tend to exhibit higher growth rate, higher photosynthetic capacity, higher specific leaf area, higher resistance to herbivores, and higher fecundity than native species of invaded communities (Daehler 2003; Pysek and Richardson 2007; Ramula et al. 2008; van Kleunen et al. 2010; Dawson et al. 2011). Contradictory results were however found between global analyses for important traits such as plant size (Hawkes 2007; van Kleunen et al. 2010), seed mass (Mason et al. 2008; Ordonez et al. 2010) and plant fecundity (Daehler 2003; Pysek and Richardson 2007). The feasibility of predicting invasiveness based on traits alone is therefore still disputed (van Kleunen et al. 2010; Moles et al. 2012).

This discussion is also particularly relevant since studies have recently suggested that species may be pre-adapted for invasion (Pysek and Richardson 2007; Schlaepfer et al. 2010; Jenkins and Keller 2011; Dostal et al. 2013). In common garden experiments, native individuals of species that have become invasive in their introduced ranges had higher germination, higher shoot-root ratios, and greater biomass production than native individuals of non-invasive exotic species (Schlaepfer et al. 2010; van Kleunen et al. 2011). These findings thus represent a new pathway in our understanding of the origins of invasiveness, and more experimental work in the native ranges involving more species and more traits is now needed. The pre-adaptation hypothesis should also be tested in the context of trait plasticity across multiple environmental gradients.

Phenotypic plasticity of invasive species

A particular case in the search of specific traits conferring invasiveness is the study of trait phenotypic plasticity, which is a major source of variation in nature, and thus an important concept in ecological and evolutionary biology. Phenotypic plasticity is the ability of genotypes to express different phenotypes in response to changing or novel climate conditions (Schlichting 1986; Sultan 2000, 2001). Plants are plastic for many traits related to structure, development, metabolic activity, morphology, physiology, phenology and reproduction (Sultan 1995; Pintado et al. 1997; Valladares et al. 2000; Sultan 2001; González and Gianoli 2004; Sánchez-Gómez et al. 2006; Portsmuth and Niinemets 2007).

In the context of plant invasion, phenotypic plasticity plays an important role by enhancing ecological niche breadth and population growth rate of invaders (Baker 1965; Sexton et al. 2002; Richards et al. 2006; Ghalambor et al. 2007; Funk 2008). Invasive species are generally more plastic for a variety of morphological and physiological traits when compared to native and non-invasive exotic species (Pattison et al. 1998; Niinemets et al. 2003; Burns and Winn 2006; Pan et al. 2006; Zhao et al. 2010; Skálova et al. 2012). This pattern has recently been summarized by Davidson et al. (2011) via a meta-analysis conducted on 75 pairs of invasive/native species and spanning several traits and a range of resource conditions.

Plasticity of morphological and physiological traits has an effect on invasiveness if it contributes to increase fitness, *i.e.* enhances survival and reproduction (van Kleunen and Fischer 2005; Ghalambor et al. 2007). In this regard, invaders are thought to benefit from plasticity as (i) Jacks-of-all-trades, when they maintain fitness across varied environmental conditions, (ii) Masters-of-some, when they are able to increase fitness under favourable conditions, or (iii) Jacks-and-Masters (Richards et al. 2006). Davidson et al. (2011) empirically analysed these scenarios, and found that the higher plasticity of invasive species was finally weakly associated with greater fitness gains in response to a resource increase. At the same time, comparisons of 20 pairs of invasive/native species showed that trait means were relatively more important than trait plasticity to explain the higher fitness of invasive over native species (Godoy et al. 2012). The relative success of invaders could thus be more dependent on differences in trait values between native and invasive species (Godoy et al. 2011; Palacio-López and Gianoli 2011). However, these results have to be currently interpreted with caution due to limited fitness data available. Overall, phenotypic plasticity can promote invasiveness by allowing exotic plant species to tolerate new environmental conditions, while the evolution of plasticity has also been shown to be beneficial in new environments (Bossdorf et al. 2008; Droste et al. 2010). The role of plasticity in shaping phenotypic variation has now to be simultaneously tested with evolutionary processes and other sources of variation such as genetic drift, environmental maternal effects, and local adaptation.

Evolutionary processes of invasions

A paradox in invasion biology is that invasive species succeed in replacing species that have had a longer time to adapt to local environmental conditions. Despite a lag period of adaptation, invasive species are indeed known to rapidly become tolerant to novel environments. Invasions thus represent opportunities to better understand evolutionary processes such as rapid adaptation, short-term evolution, and natural selection (Hänfling and Kollmann 2002; Novak 2007; Keller and Taylor 2010). This can be achieved via the use of common garden experiments and molecular analyses.

Intraspecific comparisons of quantitative genetic variation have become more and more popular in invasion biology. Based on common garden experiments, these studies have sought to determine whether invasive populations have undergone shifts towards increased growth and/or competitive ability compared to their native conspecifics (Siemann and Rogers 2001; Blumenthal and Hufbauer 2007; Droste et al. 2010). Many studies revealed genetically-based differences (genetic differentiation) in various life-history traits both between native and invasive populations and among invasive populations (Leger and Rice 2003; Bossdorf et al. 2008; Droste et al. 2010; Feng et al. 2011). For example, invasive genotypes of European *Hypericum perforatum* L. and *Lythrum salicaria* L. re-established latitudinal clines in size, fecundity and flowering across the introduced range, and thus showed rapid evolutionary response to climatic selection in North America (Maron et al. 2004, 2007; Montague et al. 2008). Invasive genotypes of *Polygonum cespitosum* Blume exhibited higher plasticity to light availability than the ones sampled 11 years before, which suggests an evolutionary change in adaptive plasticity among invasive populations during the species' expansion into open sites

(Sultan et al. 2013). Quantitative genetic studies offer therefore valuable insights into potential post-introduction evolution of populations. They cannot however allow the evaluation of more mechanistic explanations such as population genetic diversity, genetic bottlenecks, hybridization, and natural selection, which require the use of molecular analyses.

Population genetics offers a complementary approach to common garden experiments. Molecular analyses have been used for various purposes such as identifying native source populations (Williams et al. 2005; Ortiz et al. 2008), reconstructing routes and histories of invasion (Estoup and Guillemaud 2010; Gaudeul et al. 2011), comparing genetic structure between native and invasive populations (Prentis et al. 2009; Erfmeier and Bruelheide 2011), and assessing evolutionary consequences of invasions (Carroll 2007; Suarez and Tsutsui 2008). Lavergne and Molofsky (2007) for instance showed that the success of European *Phalaris arundinacea* L. in North America wetlands was not due to a single introduction of pre-adapted genotypes but rather to multiple introductions of genotypes that were redistributed and recombined into North American populations. Multiple introduction events of exotic organisms may be the rule rather than the exception (Durka et al. 2005; Genton et al. 2005; Henry et al. 2009; Pairon et al. 2010). This would balance the reduction in genetic variation that generally occurs when genotypes are introduced in new regions (Dlugosch and Parker 2008a; Estoup and Guillemaud 2010), although there are cases of invasion such as *Hypericum canariense* L. demonstrating that local adaptation can also proceed rapidly despite single introductions of genotypes and strong founder effects (Dlugosch and Parker 2008a,b). Successful invaders are therefore appropriate study cases to understand evolutionary processes over short-time periods, and their role in establishing species range limits and species interactions. Combining common garden experiments and genetic analyses can also be beneficial for the development of management strategies by identifying isolated populations that should be kept away from other populations to minimize gene flow (Estoup and Guillemaud 2010). More work should now focus on assessing adaptive evolutionary responses of populations to climate change. In this regard, invasive trees provide pertinent examples because the responses of tree species to future changes still remain speculative (Kremer 2007; Alberto et al. 2011).

Invasive trees: valuable models to understand plant invasions

Globally, forests cover one third of the land area and contain approximately 80% of terrestrial biodiversity (UN International Year of Forests 2011, http://www.un.org/en/events/iyof2011/). They strongly influence global climate and biogeochemical cycles by acting as sources and sinks of greenhouse gases (Canadell and Raupach 2008; Kolström et al. 2011). In forests, tree species are ecosystem engineers because they regulate major processes such as fixation of carbon, decomposition of organic matter, nutrient and water cycling, and degradation of toxic compounds (Sayer 2006; Aerts and Honnay 2011; Pan et al. 2011). They also moderate local temperature via canopy transpiration, affect resource availability to herb layer species, and provide nesting and sheltering cavities as well as abundant food for many vertebrate species (Gilliam and Roberts 2003; Richardson et al. 2007; Farwig et al. 2008; Lindenmayer et al. 2012). Experimental approaches are however difficult to set up in forests, and uncertainty still exists on the functional significance of tree species diversity and identity for ecosystem processes in forests (Scherer-

Lorenzen et al. 2005). Productivity in forests might finally be dependent on climate, water availability and soil fertility (Jacob et al. 2013), while significant effects of tree species identity were recently found on litter decomposition, belowground biomass, microbial community composition, and insect guild structure in temperate and tropical forests (Grayston and Prescott 2005; Vivanco and Austin 2008; Meinen et al. 2009; Plath et al. 2012). Tree species identity, and not diversity, could thus play a prominent role for ecosystem functioning.

The replacement of native by invasive tree species in both forests and grassland habitats is therefore critical. A total of 652 woody species encompassing 357 temperate and tropical trees are currently considered invasive in regions they were introduced to (Richardson and Rejmanek 2011). There are various reasons for worldwide introduction and dissemination of exotic tree species such as horticulture, forestry, food, control of erosion and driftsand, and fuelwood supply (Richardson 1998; Reichard and White 2001; Breton et al. 2008). Examples of major tree invasions include *Eucalyptus*, *Pinus* and Australian *Acacia* species in the Southern Hemisphere (Richardson and van Wilgen 2004; Becerra and Bustamante 2008; Zenni et al. 2009; Rodriguez-Echeverria et al. 2011), evergreen *Myrica faya* in montane rainforests of Hawaii (Vitousek and Walker 1989; Asner and Vitousek 2005), *Tamarix* species in arid and semiarid regions of western North America (Zavelta and Hobbes 2001; DeWine and Cooper 2010) and broadleaved *Triadica sebifera*, *Ailanthus altissima* and *Robinia pseudoacacia* in deciduous forests of the Northern Hemisphere (Keay et al. 2000; Rogers and Siemann 2002; Kowarik and Saumel 2008; Castro-Diez et al. 2009; Martin and Canham 2010). Moreover, invasive trees strongly modify nutrient cycling, hydrology, litterfall and decomposition rates of invaded ecosystems (Richardson and Higgins 1998; Le Maitre et al. 2000; Allison and Vitousek 2004; Yelenik et al. 2004). They also alter community dynamics by suppressing native keystone species and reducing native understory diversity and regeneration (Martin 1999; Fang and Wang 2011; Cuneo and Leishman 2013; Schachtschneider and February 2013). Nonetheless, there is a paucity of data on the forces driving these invasions. Few studies documented the relative importance of functional traits and evolutionary processes in the success of invasive trees. Filling these gaps would thus provide better insights on the general patterns of tree invasion dynamics, which would help to define a common framework for tree invasion biology and to establish more accurate management strategies at the local scale.

Objectives of the project

The present project seeks to understand maple tree invasion, *i.e.* to determine which dominant environmental factors, functional traits and evolutionary processes drive the success of *A. negundo* and *A. platanoides* in their introduced range. We explore the following questions:

(*i*) Do introduced populations occur at higher density and/or abundance than their native conspecifics (*cf.* home *vs.* away comparisons)? Are introduced populations well distributed regionally? It is assumed that plant survival and reproduction as well as population density and dominance of exotic species are higher in the introduced than in the native range. However, demographic processes have rarely been contrasted to test if any of the above patterns occur. The aforementioned questions are addressed to evaluate the extent of maple tree invasion, *i.e.* to quantify population increase, local dominance and range expansion of exotic maple tree populations (Chapter 1).

(*ii*) Is there a reduction in abundance or density of native species populations? Exotic plant populations have been found to negatively affect populations of co-occurring native species at the local scale. We investigate this idea for the two exotic maple tree species (Chapter 1).

(*iii*) What are the environmental factors that favour invasion? More importantly, what are the relevant functional traits that contribute to invasiveness? Abiotic factors and biotic characteristics play an important role in the success of invasive species. Moreover, identifying invasive species based on functional traits would be highly valuable for risk-assessment protocols. We identify here the particular conditions and important functional traits that drive maple tree invasion (Chapters 2 and 3).

(*iv*) Is there genetic differentiation between native and invasive populations? Do invasive populations exhibit higher phenotypic plasticity than their native conspecifics? Genetic differentiation and phenotypic plasticity are two processes that can explain successful invasion. We seek to assess the environmental and genetic determinism of the traits conferring invasiveness. This is achieved by comparing the performance of native and invasive genotypes under common environmental conditions (Chapters 4 and 5).

Overall, this approach may give insights on the link between determinants of successful invasion and species life-history strategy: do differences in species life-history strategy (*cf.* early *vs.* late-successional species) explain variation in their invasion success?

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Table 1. Description of the hypotheses proposed to explain the success of invasive species.

Driving factors and respective hypotheses	Description
Propagule pressure (PP)	
Propagule pressure (PP)	High supply and frequency of plant propagule introductions increase the chance of successful invasion. Propagules include seeds, adult plants and reproductive vegetative fragments (+)[1].
Sampling (SP)	The larger the pool of species introduced, the greater the chance it contains a species able to exploit resources and tolerate enemies more effectively than native species (+).
Abiotic characteristics (A)	
Disturbance (D)	Natural and anthropogenic disturbances increase resource levels and reset succession. Exotic species have an equal chance of success at colonization and establishment than native species (+).
Dynamic equilibrium model (DE)	Interaction between disturbance and productivity. Exotic species can establish in low disturbance-low productivity habitats but become dominant only in high disturbance-high productivity ones (+/-).
Empty niche (EN)	Exotic species have access to unused resources because of a limited number of native species (+).
Environmental heterogeneity (EVH)	The more heterogeneous a habitat is, the higher the likelihood that niches are available and can be filled by exotic species (+).
Fluctuating resource availability (FRA)	Exotic species can invade recipient communities following an increase in resource levels due to an increase in supply following disturbances or decrease in uptake by native species (+).
Habitat filtering (HF)	Exotic species are adapted to ecosystem conditions and can pass through environmental filtering. The more heterogeneous a habitat is, the more it promotes invasion (+).
Opportunity windows (OW)	Similar to EN, but here niche availability fluctuates through time and space (+).
Resource-enemy release (R-ER)	Combination of IRA and ER. Invasion can occur with only ER or IRA but is enhanced when both occurs simultaneously (+).
Biotic characteristics (B)	
Adaptation (ADP)	Exotic species are pre-adapted or adapt after introduction to new ecosystem conditions (+).
Biotic indirect effects (BID)	Gathers several indirect interaction mechanisms such as apparent competition, indirect mutualism/commensalism, exploitative competition and trophic cascades that can facilitate invasion (+).
Biotic resistance (BR)	Invasion limited or impeded by competitors and enemies of recipient communities (-).
Darwin's naturalization (DN)	Integration of several hypotheses as invasion is attributed to human interference, propagule pressure, favourable environmental conditions and community interactions (+).
Enemy of my enemy (EE)	Effects of pathogens and herbivores are stronger on native species. Generalist pathogens limit exotic species abundance but limit native competitors more (+).

Enemy inversion (EI)	Natural enemies of exotic species are also introduced into the new range where they are less efficient or have an opposite effect (+).
Evolution of increased competitive ability (EICA)	Similar to ER, but here selection acts on traits enhancing competitive ability and invasiveness (+).
Enemy release (ER)	Exotic species are released from their pathogens and herbivores when introduced into a new range, and resources previously used for defence are reallocated to growth and reproduction (+).
Enemy reduction (ERD)	Similar to ER, but here a partial and not complete release of enemies facilitate invasion (+).
Facilitation (F)	Native species facilitate colonization and establishment of exotic species in recipient communities (+).
Global competition (GC)	The larger the pool of species introduced, the greater the chance it contains a competitive species (+).
Invasional meltdown (IM)	Direct or indirect symbiotic relationships between exotic species facilitate invasion (+).
Increased susceptibility (IS)	Lack of defence make exotic species susceptible to enemies in the new range and low genetic diversity prevents them from adapting to enemies (-).
Ideal weed (IW)	Life history, characteristics and traits of species facilitate their invasion of recipient communities (+).
Limiting similarity (LS)	Exotic species are functionally distinct from native species, which limits interspecific competition and allow them to have access to unused resources (empty niche) (+).
Missed mutualisms (MM)	Species introduced into a new range lose beneficial mutualistic relationships which prevents invasion (-).
New associations (NAS)	New relationships between exotic and native species facilitate or prevent invasion (+/-).
Novel weapons (NW)	Exotic species release allelopathic compounds that inhibit native species and facilitate invasion (+).
Reckless invader (RI)	Characteristics of exotic species that facilitate invasion under certain conditions may be disadvantageous when conditions change (+).
Specialist-generalist (SG)	Success of invasion is maximized when enemies in the new range are specialists and native mutualists are generalists (+).

[1] Effect predicted by the hypothesis on the success of invasion: (+): positive (*i.e.* facilitative) effect; (-): negative (*i.e.* inhibitive) effect; (+/-): positive or negative effect depending on conditions.

Key references of hypotheses are as follows (see also Appendix 2): ADP: Duncan and Williams (2002); BID: Callaway et al. (2004); BR: Levine et al. (2004); D: Mack et al. (2000); DE: Huston (2004); DN: Darwin (1859), Pysek and Richardson (2006); EE: Eppinga et al. (2006); EI: Colautti et al. (2004); EICA: Blossey and Nötzold (1995); EN: Levine and D'Antonio (1999); ER: Keane and Crawley (2002); ERD: Colautti et al. (2004); EVH: Melbourne et al. (2007); F: Bruno et al. (2003); FRA: Davis et al. (2000); GC: Alpert 2006; HF: Melbourne et al. (2007); IM: Simberloff and Holle (1999); IS: Colautti et al. (2004); IW: Elton (1958); LS: Vitousek et al. (1987); MM: Mitchell et al. (2006); NAS: Callaway et al. (2004); NW: Callaway and Aschehoug (2000); OW: Johnstone (1986); PP: Lonsdale (1999); R-ER: Blumenthal (2006); RI: Simberloff and Gibbons (2004); SG: Callaway et al. (2004); SP: Crawley et al. (1999).

Table 2. Review of the studies that used reciprocal common gardens to test evolutionary changes in invasive species.

Reference	Studied species	Number and location of common gardens
Genton et al. 2005	*Ambrosia artemisiifolia* L.	1 in the native range (Ontario, Canada) 3 in the introduced range (France)
Hierro et al. 2013	*Centaurea solstitialis* L.	1 in the native range (Turkey) 1 in the introduced range (Argentina)
Maron et al. 2004a	*Hypericum perforatum* L.	1 in the native range (Spain) 1 in the introduced range (Washington, USA)
Maron et al. 2004b	*Hypericum perforatum* L.	2 in the native range (Spain and Sweden) 1 in the introduced range (Washington, USA)
Maron et al. 2007	*Hypericum perforatum* L.	1 in the native range (Spain) 1 in the introduced range (Washington, USA)
Williams et al. 2008	*Cynoglossum officinale* L.	1 in the native range (Germany) 1 in the introduced range (Montana, USA)

Table 3. List of invasive tree species on which invasion hypotheses were tested. A literature review was conducted on Web of Science for the terms [tree* invas* name of the hypothesis] and using the article of reference of each hypothesis. All published studies up until 17 June 2013 were searched. See Appendix 3 for the complete list of studies.

Driving factors and respective hypotheses	Time tested	Invasive tree species studied
Propagule pressure (P)		
Propagule pressure (PP)	16	*Acacia cyclops*, *Acacia saligna*, *Acer negundo*, *Acer platanoides*, *Ailanthus altissima*, *Celtis* sp, *Cordia alliodora*, *Larix decidua*, *Pinus* spp[1], *Prunus serotina*, *Pseudotsuga menziesii*, *Quercus rubra*, *Rhamnus cathartica*, *Robinia pseudo-acacia*, *Schinus molle*, *Schinus terebinthifolius*
Sampling (SP)	0	
Abiotic characteristics (A)		
Disturbance (D)	15	*Acacia dealbata*, *Acacia longifolia*, *Acacia saligna*, *Ailanthus altissima*, *Eriobotrya japonica*, *Gleditsia triacanthos*, *Homalanthus populifolius*, *Ligustrum lucidum*, *Paraserianthes lophantha*, *Paulownia tomentosa*, *Pinus* spp, *Pittosporum undulatum*, *Populus x canescens*, *Prosopis caldenia*, *Prunus serotina*, *Quercus robur*, *Solanum mauritianum*, *Ulmus pumila*
Dynamic equilibrium model (DE)	0	
Empty niche (EN)	6	*Ailanthus altissima*, *Pittosporum undulatum*, *Prunus serotina, Robinia pseudo-acacia, Rhamnus cathartica*
Environmental heterogeneity (EVH)	0	
Fluctuating resource availability (FRA)	13	*Acacia longifolia*, *Acer platanoides*, *Alstonia macrophylla*, *Bischofia javanica*, *Cinnamomum verum*, *Melaleuca quinquenervia*, *Psidium cattleianum*, *Sandoricum koetjape*, *Syzygium jambos*, *Tabebuia pallida*, *Tamarix ramosissima*, *Triadica sebifera*
Habitat filtering (HF)	0	
Opportunity windows (OW)	0	
Resource-enemy release (R-ER)	0	
Biotic characteristics (B)		
Adaptation (ADP)	2	*Acer negundo*, *Acacia cyclops*, *Acacia longifolia*, *Acacia melanoxylon*, *Acacia saligna*, *Paraserianthes lophantha*
Biotic indirect effects (BID)	0	

Biotic resistance (BR)	3	*Acer negundo*, *Pinus radiata*, *Tamarix* spp
Darwin's naturalization (DN)	6	*Acacia cyclops*, *Coniferae* sp[2], *Melaleuca quinquenervia*, *Pseudotsuga menziesii*
Enemy of my enemy (EE)	0	
Enemy inversion (EI)	0	
Evolution of increased competitive ability (EICA)	19	*Melaleuca quinquenervia*, *Triadica sebifera*
Enemy release (ER)	21	*Acer negundo*, *Acer platanoides*, *Adenanthera pavonia*, *Ardisia elliptica*, *Eugenia uniflora*, *Paulownia tomentosa*, *Phellodendron amurense*, *Pinus radiata*, *Prunus serotina*, *Rhamnus cathartica*, *Swietenia macrophylla*, *Triadica sebifera*
Enemy reduction (ERD)	0	
Facilitation (F)	15	*Acer negundo*, *Acer platanoides*, *Eucalyptus globulus*, *Ligustrum lucidum*, *Pinus ponderosa*, *Pinus radiata*, *Pinus taeda*, *Pseudotsuga menziesii*, *Pyracantha angustifolia*, *Rhamnus cathartica*, *Schinus molle*, *Triadica sebifera*
Global competition (GC)	0	
Invasional meltdown (IM)	2	*Morella faya*, *Pinus halepensis*
Increased susceptibility (IS)	0	
Ideal weed (IW)	0	
Limiting similarity (LS)	0	
Missed mutualisms (MM)	0	
New associations (NAS)	1	*Albizia julibrissin*
Novel weapons (NW)	13	*Acacia dealbata*, *Acer platanoides*, *Ailanthus altissima*, *Robinia pseudo-acacia*, *Schinus terebinthifolius*, *Tamarix ramosissima, Triadica sebifera*
Reckless invader (RI)	0	
Specialist-generalist (SG)	0	

[1] Invasive *Pinus* species in the Southern Hemisphere include *P. albicaulis*, *banksiana*, *canariensis*, *cembroides*, *contorta*, *coulteri*, *edulis*, *flexilis*, *gerardiana*, *greggii*, *halepensis*, *jeffreyi*, *kesiya*, *lambertiana*, *luchuensis*, *massoniana*, *merkusii*, *monophylla*, *monticola*, *mugo*, *muricata*, *nigra*, *patula*, *pinaster*, *pinea*, *ponderosa*, *radiata*, *resinosa*, *roxburghii*, *sabiniana*, *strobus*, *sylvestris*, *taeda*, *virginiana*.

[2] *Coniferae* species considered naturalized in Europe include *Araucaria araucana*, *Chamaecyparis pisifera*, *Cryptomerica japonica*, *Cupressus arizonica*, *C. lusitanica*, *C. macrocarpa*, *C.* x *leylandii*, *Juniperus chinensis*, *J. virginiana*, *Platycladus orientalis*, *Abies balsamea*, *A. concolor*, *A. grandis*, *A. lasiocarpa*, *A. procera*, *Cedrus atlantica*, *Larix gmelinii*, *L. kaempferi*, *L. laricina*, *L.* x *marschlinsii*, *Picea engelmannii*, *Pi. mariana*, *Pi. pungens*, *Pi. sitchensis*, *P. banksiana*, *P. ponderosa*, *P. radiata*, *P. rigida*, *P. strobus*, *P. wallichiana*, *P.* x *rotundata*, *Pseudotsuga menziesii*, *Tsuga canadensis*, *Sequoia sempervirens*, *Metasequoia glyptostroboides*, *Sequoiadendron giganteum*, *Taxodium distichum*.

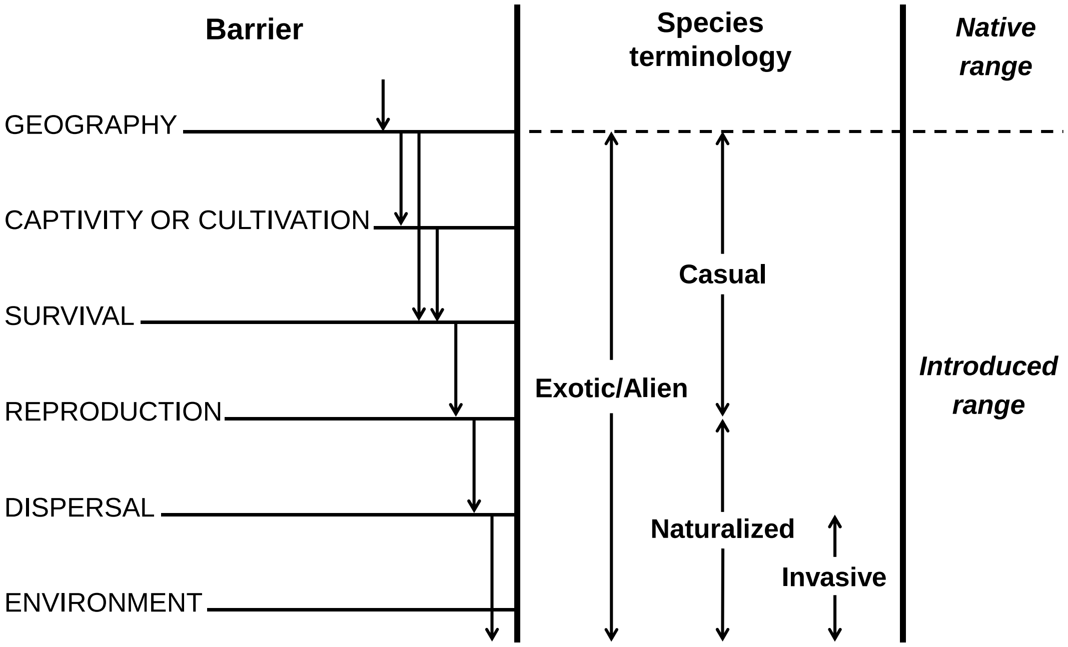

Fig. 1. The process of biological invasions (modified from Pysek and Richardson 2007 and Blackburn et al. 2011). It is divided into a series of barriers or stages that a species must overcome to pass on to the next stage. Species are referred to by different names according to the stage they have reached. Species referred to as exotics were introduced either intentionally or accidentally into a new range whereas those referred to as aliens were introduced intentionally by humans only.

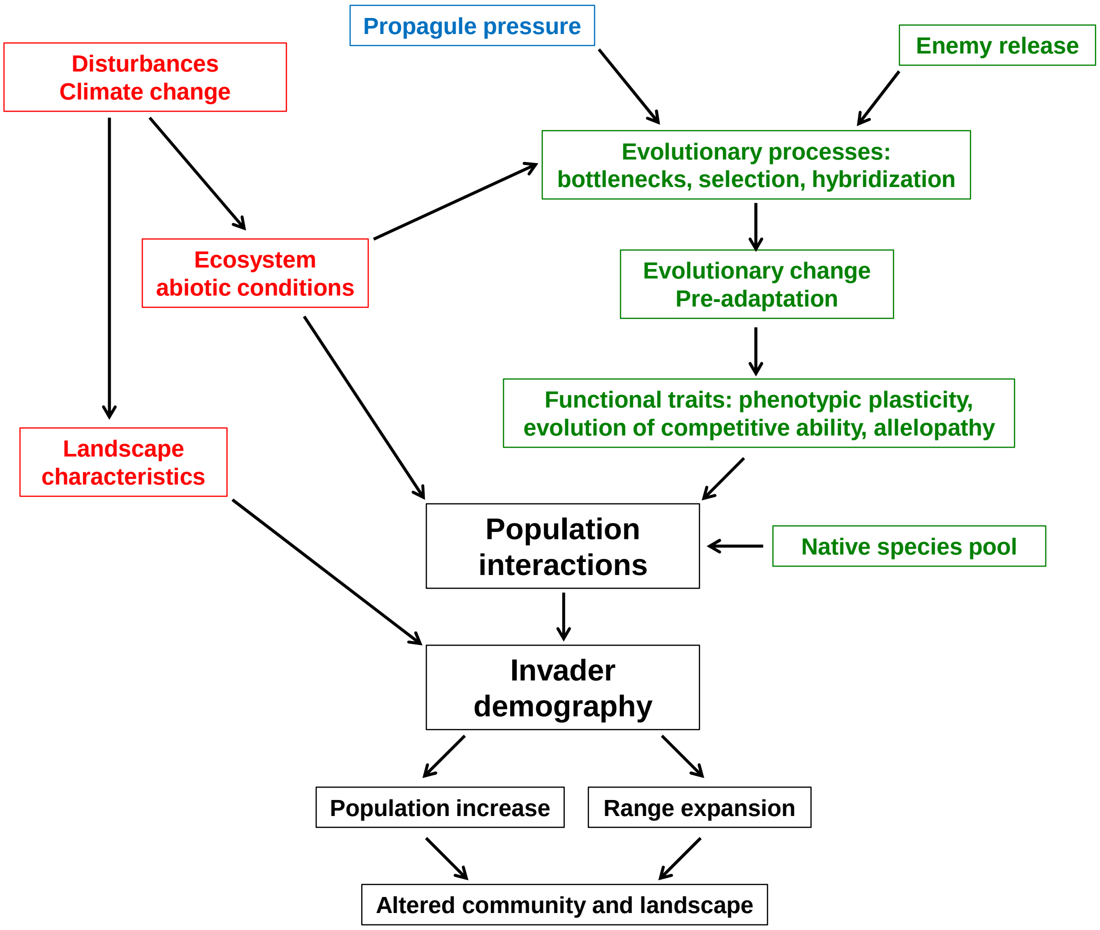

Fig. 2. Conceptual synthetic framework based on ecological and evolutionary processes (adapted from Gurevitch et al. 2011). This illustrates how propagule pressure (in blue), abiotic characteristics (in red) and biotic characteristics (in green) interact to drive invasions. Transitions between processes and states are indicated by arrows.

Chapter 1

A biogeographical approach to estimate the extent of invasion of two exotic trees

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Abstract

Quantitative comparisons of distribution and abundance of exotic species in their native and non-native ranges represent a first step when studying invaders. However, this approach is rarely applied _ particularly to tree species. Using biogeographical contrasts coupled with regional dispersal surveys, we assessed whether two exotic maple tree species, *Acer negundo* and *Acer platanoides* , can be classified as invasive in the non-native regions surveyed. We also examined the importance of biogeography in determining the degree of invasion by exotic species using this reciprocal approach. Local-scale surveys were conducted in a total of 34 forests to compare density, relative abundance, age structure of native and introduced populations, and whether the two introduced maple species negatively affected native tree species density. Regional-scale surveys of a total of 136 forests were then conducted to assess distribution in the introduced regions. Introduced populations of *A. negundo* were denser than populations measured in their native range and negatively related to native tree species density. Age structure did not differ between regions for this species. At the regional scale, this species has invaded most of the riparian corridors sampled in France. Conversely, the density of *A. platanoides* introduced populations was similar to that of native populations and was not related to native tree species density. Although seedling recruitment was higher away than at home, this species has invaded only 9% of the forests sampled in southern Ontario, Canada. Although reported invasive, these two exotic maple species differed in their relative demographic parameters and regional spread. *Acer negundo* is currently invasive in southern France while *A. platanoides* is not aggressively invasive in southern Ontario. Importantly, this study effectively demonstrates that biogeography through structured contrasts provide a direct means to infer invasion of exotic species.

Introduction

Invasive species can significantly impact native communities and ecosystems (Vitousek et al. 1996, Mack et al. 2000). The degree of invasion either locally or regionally is however rarely quantified to determine how different populations of such species are between their native and non-native ranges (Hinz and Schwarzlaender 2004, but see Grigulis et al. 2001, Paynter et al. 2003, Jakobs et al. 2004, Pergl et al. 2006, Beckman et al. 2009). Perhaps the most effective method proposed to assess the relative degree of invasion would be to biogeographically contrast the density and relative abundance of the introduced species in its home and away range (Hierro et al. 2005). Whilst this approach has been successfully applied to the study of soil biotic effects on native communities (Reinhart et al. 2003, Reinhart and Callaway 2004) and plant evolving adaptations (Rogers and Siemann 2005, Williams et al. 2008), it has nonetheless rarely been applied directly to estimates of relative population density and regional spread, either because plant growth differences between ranges seem obvious and such studies unnecessary or because comparative studies across continents are difficult and costly (Hinz and Schwarzlaender 2004). We define invasive species here as exotic species which must exhibit ‘important ecological differences’ between native and non-native ranges (Elton 1958, Inderjit 2005). Differences can include increased population size or density, plant vigor, reproductive output, or seedling establishment (Hinz and Schwarzlaender 2004), and there is also a general consensus in the literature that exotics behaving similarly in both its ranges are not invaders (Crawley 1987, Chapin et al. 2000, Sakai et al. 2001). These definitions do not include impacts or the relative effects of the invader. To date, invasive species are mainly defined in biogeographical contrasts (Valery et al. 2008, Wilson et al. 2009) and refer to allochthonous plants with human-mediated dispersal pathways (Richardson et al. 2000, Colautti and MacIsaac 2004, Pysek et al. 2004, Richardson and Pysek 2006).

We propose that unambiguous quantification of the distribution and abundance of introduced species in their native and non-native ranges is a crucial first step in studying invasive plant species and potentially determining whether a given species is invasive in its introduced range at this point in time. Given that trees are very long-lived and ecosystem engineers strongly shaping both the function and the biodiversity of an ecosystem (Jones et al. 1994, Richardson 1998), this method should be particularly amenable to and useful for explaining the degree of invasion of tree species. Substitutions between different tree species within a forest ecosystem also dramatically alter function and composition (Bertin et al. 2005, Zobel et al. 2006), and invasion by tree species thus represents one of the most aggressive changes to a native community or ecosystem (Richardson 1998). Hence, two tree species reciprocally introduced into the other's range is an ideal case study to test this method.

Here, biogeographical contrasts were applied using spatially-structured local density surveys and regional surveys for two maple tree species - *Acer negundo* and *Acer platanoides* - both of which are reciprocally native in one range and introduced into the range of the other where they are assumed invasive. This is a perfect opportunity to explore biogeography as it relates to invasion and extends the previous work of Reinhart and Callaway in 2004. The following three predictions were thus tested to examine the overarching general hypothesis that biogeographical contrasts are an effective means to describe invasiveness of a plant species: 1) if a species is invasive, the introduced populations occur at higher density and abundance relative to the native conspecifics, i.e. there are intraspecific inter-regional differences in density. 2) If a species is invasive, it must at some even minor level negatively impact the density of the native species due to interference or displacement/saturation. 3) If a species is to be considered invasive, the regional spread of the species in the novel region should be at least 10%, i.e. more than 1 in 10 communities surveyed should have the introduced species present at even low densities of juveniles or adult trees. We recognize there are limitations to or counter-arguments against these three predictions but nonetheless propose that taken together they definitely demonstrate that relative differences in the density and extent of presence within a novel region can be used to infer invasiveness.

Material and Methods

Study species and habitat descriptions

Acer negundo L. (Manitoba maple), native to Northeastern America has been introduced into many regions throughout Europe since 1688 (Medrzycki 2007). It often occurs in dense monospecific stands and grows in disturbed sites, along roadsides, in abandoned fields (Medrzycki 2007). It is also frequently found in the riparian zones of Southern Europe and especially in France (Rhone, Garonne, Adour rivers), characterized by a high rate of disturbance such as flood and high soil nutrient levels (Tabacchi and Planty-Tabacchi 2003).

Acer platanoides L. (Norway maple), native to Europe, has become a commonly planted street tree in North America since its importation to Philadelphia in the mid-to-late 1700's (Spongberg 1990), because of its ability to tolerate stressful urban environments combined with its ease of propagation (Nowak and Rowntree 1990). From this widespread planting, it has become naturalized and has spread into urban woodlands (Bertin et al. 2005) as well as intact forests (Webb and Kaunzinger 1993) wherein it has been shown to reduce understorey biodiversity (Wyckoff and Webb 1996). This species is commonly considered invasive in northeastern United States forests (Fang 2005, Martin and Marks 2006, Wangen and Webster 2006).

The natural habitats of each maple tree species were surveyed in both the native and non-native ranges. The native habitats sampled in Southern Ontario, Canada for presence of *Acer negundo* were broadleaf deciduous forests dominated by *Acer saccharum*, *Cornus canadensis*, *Fraxinus americana* and *Prunus nigra* whilst forests sampled in Southern France for presence of *Acer platanoides* were broadleaf deciduous habitats dominated by *Quercus pubescens*, *Fraxinus angustifolia* and *Carpinus betulus*. Similarly, non-native forests sampled were the type of habitats commonly invaded by *Acer negundo* in France and *Acer platanoides* in Canada. Thus, forests visited in Southern France were riparian deciduous forests dominated by native *Salix alba*, *Populus nigra*, *Fraxinus excelsior* and *Fraxinus angustifolia*. In Canada, sites were broadleaf deciduous forests dominated by native *Acer saccharum*, *Acer negundo*, *Cornus canadensis* and *Fraxinus americana*.

Density and relative abundance

Spatially-structured density surveys were conducted in both native and non-native ranges for each maple tree species. In total, 20 forests were surveyed in Southern Ontario, Canada and 14 in Southern France (Appendices 4-7). Within each forest, population densities were estimated not only for the introduced maple tree species but also for the native tree species occurring in the non-native range recipient communities. *Acer negundo* populations were sampled in 16 forests in Canada and 7 in France and *Acer platanoides* populations in 10 forests in Canada and 7 in France.

All the population densities were estimated with the same T-square method, a plotless density estimator based on tree-to-nearest-tree measurements (Byth 1982). Specifically, introduced and native tree stem densities were assessed using 600 m transects with regular sampling at 3 m intervals. Both the distance from the transect to the nearest target tree species and the distance from that individual to its closest neighbour were recorded at each interval (Krebs 1999, Steinke and Hennenberg 2006). This distance-based sampling technique provides an accurate estimate of both density and degree of spatial aggregation (Steinke and Hennenberg 2006). Moreover, the life-stage of each stem sampled was also recorded as seedlings (< 0.5 m in height), juveniles (> 0.5 m but < 3 m) or reproductively mature adults (> 3 m).

Species relative abundances were estimated by dividing the number of exotic maple tree individuals by the total number of individuals sampled in each forest. Similarly, we calculated life-stage relative abundances by dividing the number of adults, juveniles and seedlings of a given species by the total number of adults, juveniles and seedlings sampled in each forest, respectively.

Regional spread

To assess the regional extent of each maple tree species in its non-native range, a total of 66 forests were surveyed in Southern Ontario for presence of *Acer platanoides* and 70 in Southern France for presence of *Acer negundo* throughout a similar region area of 30,000 km^2 (Appendices 8-10). The sampled forests were chosen when they met the three following criteria: *(i)* being within the defined region area, *(ii)* specifically matching the type of habitat usually invaded by the target maple tree species, and *(iii)* having an area of at least 10 ha. Each forest was then classified as uninvaded (species absent), invaded (species present with up to 5 individuals, whatever life-stage) or highly invaded (population established with at least 15 adults). Albeit a crude categorical measure, this survey facilitated rapid and broad assessments of invasion within each forest via two 700 m transects 100 m apart. This scale provided a good estimator of presence and included both edge and central sampling at a site.

Statistical analyses

Generalized linear models were used to test the effects of maple species, range, native tree species diversity (estimated via the Shannon index), and appropriate interaction effects on both the density and relative abundance of these exotic maple species. Tukey LSD *post hoc* contrasts were then used to ascertain specific, within factor significant differences at alpha $p < 0.05$. For each exotic maple species, variation in frequency of stems amongst age categories pooled across sites within region was also analysed using Chi-square tests with region and age-class as factors. Standard linear regressions were then used to examine the effect of introduced maple tree density on native tree density. A 2 x 2 Chi-square test was used to examine the regional spread of *A. negundo* in Southern France and *A. platanoides* in Southern Ontario, Canada. All statistics were performed with JMP 9 ver. 9 (SAS).

Results

Density and relative abundance of the exotic maple species

There were significant species, range, and species by range interaction effects on both invasive species density and relative abundance between the forests sampled whilst the diversity of the native tree species did not significantly predict these two estimates of invasion (GLMs, Table 1). The density and relative abundance of *A. negundo* was significantly greater in the non-native range than in the native range whilst *A. platanoides* did not differ in either measure between the two ranges (Table 1 with Tukey *post hoc* contrasts, Fig. 1). The representation of age categories did not differ between ranges for *A. negundo* (Chi-square test, $\chi^2 = 4.3387$, $P = 0.1183$, d.f. = 2, Fig. 2), but *A. platanoides* age categories did significantly differ with more seedlings and saplings and a lower number of total trees in the non-native range (Chi-square test, $\chi^2 = 25.9442$, $P < 0.0001$, d.f. = 2, Fig. 2). There was a significant negative effect of the density of introduced *A. negundo* populations on the density of native tree species in France (Linear regression, $r^2 = 0.91$, $P = 0.0008$, d.f. = 6, Fig. 3) but no effect of the introduced *A. platanoides* populations on native tree species in Canada (Linear regression, $r^2 = 0.09$, $P = 0.38$, d.f. = 9, Fig. 3). Importantly, there were no significant effects of either maple species on other native species in their respective home ranges (Linear regressions, $r^2_{A.\ negundo} = 0.03$, $P = 0.55$, d.f. = 1; $r^2_{A.\ platanoides} = 0.02$, $P = 0.78$, d.f. = 1).

Regional distribution

The regional spread of *A. negundo* in Southern France was significantly different from that of *A. platanoides* in Southern Ontario, Canada (Chi-square test, χ^2 = 13.6969, P = 0.0011, d.f. = 2). In Southern France, most of the riparian corridors surveyed at the regional scale were invaded by *Acer negundo* (Fig. 4). The species formed monospecific stands along Adour and Dordogne Rivers, whilst the downstream on the Garonne River only was uninvaded (Appendix 8). In Southern Ontario, 27% of the broadleaf deciduous forests surveyed were uninvaded by *A. platanoides*. In contrast, only 9% of the forests were found highly invaded (Fig. 4) although no monospecific stands of *A. platanoides* were observed.

Discussion

The objective of this study was to test biogeographical contrasts as a means to infer extent of invasion using two exotic maple tree species. To do this, three predictions were tested for each of these two tree species. Introduced populations of *A. negundo* were denser than their native populations, negatively impacted the density of native tree species, and were extensively dispersed throughout the introduced region. In contrast, introduced populations of *A. platanoides* were not found at higher densities or abundances relative to the native conspecifics. There was also no evidence for negative impacts of *A. platanoides* on native tree densities, and this species had a very limited regional spread in the introduced range. Hence, the assumption that these two species are invasive in the reciprocal introduced ranges is supported for only one of the two species, i.e. all three predictions were satisfied for *A. negundo* but none of the three supported for *A. platanoides*. This study successfully demonstrated the importance of a biogeographical approach using local-scale demographic comparisons and regional dispersal surveys in determining whether exotic species can be considered invasive in their non-native range. Consequently, we propose that this methodology can be used as a basic starting point to define whether species are invasive at a given point in time within a novel region - at least using definitions associated with abundance or spread and not effects. By way of analogy, we view this approach as a facile diagnostic tool that allows ecologists or managers to quickly identify the species, symptomatically at least, that are invasive. This of course does not preclude or replace studies of mechanism, causation, or ecosystem-level effects but instead provides the means to decide whether further action is needed. The primary strength of this method is thus that density is easily measured and unequivocal in terms of its meaning, i.e. more non-native trees within a community is not desirable. However from a management and advocacy perspective, the primary limitation is that small population sizes do not necessarily imply small effects or that the particular non-native species cannot become invasive. In summary, we recommend that the density differences of a potential invasive species (between regions and relative to the natives) be emphasized versus population size per se since even small advantages may be indicative of a future increase.

The tree species *A. negundo* is clearly invasive in France with relatively higher densities and abundances than its native conspecifics. Introduced plants are often found at higher densities in the introduced ranges (Paynter et al. 2003, Reinhart et al. 2003, Jakobs et al. 2004, Vila et al. 2005, Herrera et al. 2011). Admittedly, differences in density do not guarantee impacts or invasiveness, but it can be an excellent tool to infer invasion provided the surveys are comprehensive and if exotic densities are relatively high since interference is then much more likely. Reinhart and Callaway (2004) similarly found differences in *A. negundo* in one population from the native range (Wisconsin, USA) relative to one population in the non-native range (Sablons, France) region, and they interpreted this finding as support for the enemy release hypothesis since a positive effect of the soil biota associated with the dominant native heterospecifics was measured (Reinhart and Callaway 2004). This study illustrates that even limited biogeographical contrasts can be powerful tools to assess invasion if a potential mechanism is measured concomitantly. While we did not take that approach in this study since the goal was to assess extent of invasion and not mechanism, coupling measurements of other factors at expanded scales would be a logical step including direct and indirect facilitation effects by native species and conspecifics (Saccone et al. 2010b), higher seedling survival under shade environments (Saccone et al. 2010a), or greater phenotypic plasticity for growth than native riparian tree species in response to changes in nutrient availability. Hence, integrating or coupling at least some aspects of the two approaches common in the invasion literature, i.e. more detailed mechanistic studies with broad-scale biogeographical surveys, would significantly increase our ability to describe whether a given exotic species is invasive and assess causal factors at the same time.

Conversely and surprisingly, the tree species *A. platanoides* is not currently invasive in southern Ontario in spite of numerous studies assuming invasion in the adjacent regions such as New York State, USA just south of the study sites herein (Martin and Marks 2006, Adams et al. 2009). There are several possible explanations. Ecological factors such as human disturbance may regulate populations similarly in both ranges for *A. platanoides* and naturalization may not necessarily involve evolutionary changes (Firn et al. 2011). Introduced individuals may not be better interspecific competitors relative to their native conspecifics (Vila et al. 2005), and the size of the recipient habitats available for the species may be too variable and limited, i.e. the forests in southern Ontario are very fragmented (Ebeling et al. 2008). The enemy release hypothesis (ERH) has also been invoked as an explanation for higher introduced population densities or growth relative to the native conspecifics (Keane and Crawley 2002, Wolfe 2002, Vila et al. 2005). Using a large herbivore-load survey in both ranges of *A. platanoides*, Adams et al. (2009) found that introduced populations did enjoy a significant decrease in foliar-insect herbivory relative to the native conspecifics. However, Morrison and Mauck (2007) did not find support for ERH when comparing herbivory between *A. platanoides* and the native *Acer saccharum*. Consequently, the reduction in herbivory pressure is likely not universal and differs between regions within the introduced range. Hence, herbivore loads associated with *A. platanoides* may differ between southern Ontario and more southern extents of invasion. A final alternative mechanism documented in this study and others is the negative distance and density-dependent inhibition of seedling recruitment of *A. platanoides* under conspecifics (Gomez-Aparicio et al. 2008, Martin and Canham 2010). This does not necessarily mean that this species will not become invasive in southern Ontario but does indicate that at this point in time effective management should be applied. Overall, comparisons of population demographic parameters can be used not only to determine the influence of population-based advantages such as enemy release or allelopathic compounds in the establishment and proliferation of exotic species (Firn et al. 2011), but also as an approximate guide to the level of intervention or set of management tools to be applied which is the case for this tree species. Interestingly, the differences in the relative success of invasion by these two reciprocal maples also relates to length of time since introduction. Whilst these events are not precisely documented, a 100-yr difference between *A. negundo* introductions into Europe/France versus *A. platanoides* into NA/Canada may at least partially explain the differences in density we detected with additional time providing opportunity for increases in tree density. Whilst the diagnostic tool does not indicate that *A. platanoides* is currently invasive, it would of course be prudent to implement prevention since other novel regions have been successfully invaded by this species and since in time there is no reason to expect decreases without intervention.

Successful plant invasions are often related to traits such as early and effective reproduction (Rejmanek and Richardson 1996, Grigulis et al. 2001). Studies of the age structure of a population particularly in trees provide insight into regeneration and seedling establishment patterns (Paynter et al. 2003). Population age structure did not diff er between the native and non-native regions for *A. negundo*, which means that the success of that species may not be attributed to increased seedling recruitment or that such recruitment may be limited by the availability of viable seeds and safe sites (Grigulis et al. 2001, Erfmeier and Bruelheide 2004). In contrast, introduced populations of *A. platanoides* had a greater percentage of seedlings and saplings, and in this case, germination may be influenced by both more suitable environmental conditions in the non-native regions and the genetic constitution of seeds (Erfmeier and Bruelheide 2005). The lower percentage of adult trees observed in Southern Ontario can indicate a more recent introduction event into that region relative to the northeastern USA and thus this species is still in the initial phases of colonization. More likely however is that those forests in this region have lower rates of disturbance and the duration of suppression-and- release intervals currently limit species recruitment into the canopy (Martin et al. 2009). Importantly, higher native tree densities in Canada may also provide less opportunity for invasion due to interference or site pre-emption. In invaded urban woodlands of Massachusetts, USA, Bertin et al. (2005) found that *A. platanoides* was common at all size classes which indicates that this species can certainly become invasive in similar forests to the ones sampled herein. Several factors such as seed bank, soil disturbance, and seedling survival influence seedling and sapling recruitment (Herrera et al. 2011), and there is no reason to expect that the species will not become invasive if management practices are not changed or active intervention applied. *Acer platanoides* is shade tolerant with seedlings well adapted to closed canopies and they can persist for long periods in the understory layer (Webster et al. 2005, Martin and Marks 2006). Similarly, in comparison with the native *A. saccharum*, *A. platanoides* seedlings have greater winter survival (Morrison and Mauck 2007). Hence, examining the traits for this species suggests that application of biogeographical contrasts only once can fail to capture the long-term potential of a species to become invasive, and consequently, a reasonable addendum to the method is to either repeat or explore traits.

Lastly, whilst not the primary focus of this study, the two maple species differed in their impacts on recipient native communities with negative impacts of *A. negundo* and no impact at this point in time by *A. platanoides*. The main value of testing this prediction is to heuristically explore invasiveness using biogeography in concert with the other two predictions. Nonetheless, the negative impact of *A. negundo* on native tree species density supports (at least correlatively) the hypothesis that invasions negatively affect native species richness and abundance (Tilman 1997, Foster et al. 2002). Since the recruitment of *A. negundo* seedlings is facilitated by their adult conspecifics (Saccone et al. 2010b), this species directly eliminates seedlings of native species by interference due to density-dependent competition (Wilson 2007, Brooker and Kikvidze 2008). However, the second species tested, *A. platanoides,* is likely not directly competing with natives at this point in time but other studies have shown that it can eventually do so via reduced seedling and sapling density and abundance in areas invaded by this species in the USA (Martin 1999, Fang 2005). Stands dominated by *A. platanoides* are more compositionally homogeneous and less diverse due to a reduction of the regeneration of dominant canopy species (Reinhart et al. 2005) whilst densities of *A. platanoides* seedlings are higher beneath conspecific adults than beneath native species (Wyckoff and Webb 1996, Reinhart et al. 2006). These other studies support this study given that a low number of adults have already reached the canopy in the southern Ontario forests sampled which limits both their facilitative effects on conspecific seedlings and their suppressing effects on native populations. Hence, this particular biogeographical prediction does have a limited and useful capacity to cursorily speak to impacts.

Long-distance dispersal is a key process in the range expansion of many invasive species (Pysek and Hulme 2005). In addition to local scale demographic comparisons, investigations of exotic species distribution at regional scales thus provide an assessment of population dynamics and highlight the influence of factors such as dispersal capability, landscape connectivity, and habitat fragmentation (Pauchard and Shea 2006, Kuhman et al. 2010). Except for the downstream site on the Garonne River in France where the high salinity inhibits its establishment, *A. negundo* is invading most of the floodplains surveyed at the regional scale in southern France which is consistent with previous studies from other river valleys in southern and eastern Europe (Tabacchi and Planty-Tabacchi 2003, Medrzycki 2007). Regional long-distance dispersal of non-native species is attributed to the interaction of natural processes and the invaders (Pauchard and Shea 2006). For instance, riparian systems are more prone to invasions than the surrounding landscape because of increased propagule transport by water and regular physical disturbances such as flooding (Pysek and Prach 1993, Kowarik and Saumel 2008). Given that hydrochory provides an effective dispersal vector for primarily wind-dispersed exotic tree species, *A. negundo* invasion is expected to increase in European riparian corridors (Saumel and Kowarik 2010). This is a compelling set of findings which suggests that it will continue to expand in Europe provided suitable environments and propagule pressure presumably due to the high levels of disturbance in these ecosystems. Although present in most of the stands surveyed in southern Ontario, Canada, *A. platanoides* was found to be invading only a few local forests. These regional contrasts are thus consistent with the first records that reported it as naturalized and potentially invasive in that region (Dunster 1990, Larson 1996). This begs the question if only the regional-level biogeographical contrasts can be used to infer invasion or if the more detailed demographic sampling need be applied. Previous research has shown that factors driving invasion vary according to the scale of analysis (Stohlgren et al. 2002, Knight and Reich 2005). At the local scale for instance, diversity of native species limits invasibility (Levine 2000, Von Holle 2005) while exotic plants respond to connectivity and habitat fragmentation at the landscape scale. Consequently, both local and regional biogeographical scales also need to be considered (Kuhman et al. 2010) since regional surveys provide extent estimate and local surveys provide intensity estimates.

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Table 1. Generalized Linear Model results for density and relative abundance of maple tree populations; *n* = 16 and 7 populations for *Acer negundo* in Canada and France, respectively; *n* = 10 and 7 populations for *Acer platanoides* in Canada and France, respectively.

		Population-level		
Source of variation	d.f.	χ^2	*P*-value	*Post hoc*
Density				
Species	1	9.5406	0.0020	AN > AP
Range	1	9.9898	0.0016	I > N
Species x range	1	7.3552	0.0067	I(AN) > N(AN), I(AP), N(AP)
Shannon's H'	1	0.0817	0.7750	
Relative abundance				
Species	1	184.6909	< 0.0001	AN > AP
Range	1	108.4653	< 0.0001	I > N
Species x range	1	13.9469	0.0002	I(AN) > N(AN), I(AP), N(AP)
Shannon's H'	1	0.0026	0.9587	

Bold numbers indicate significant species and range effects ($P < 0.05$). The results of the Tukey *post hoc* tests indicate the direction of the significant differences between levels of each factor. AN, *Acer negundo*; AP, *Acer platanoides*; Inv, invasive range; Nat, native range.

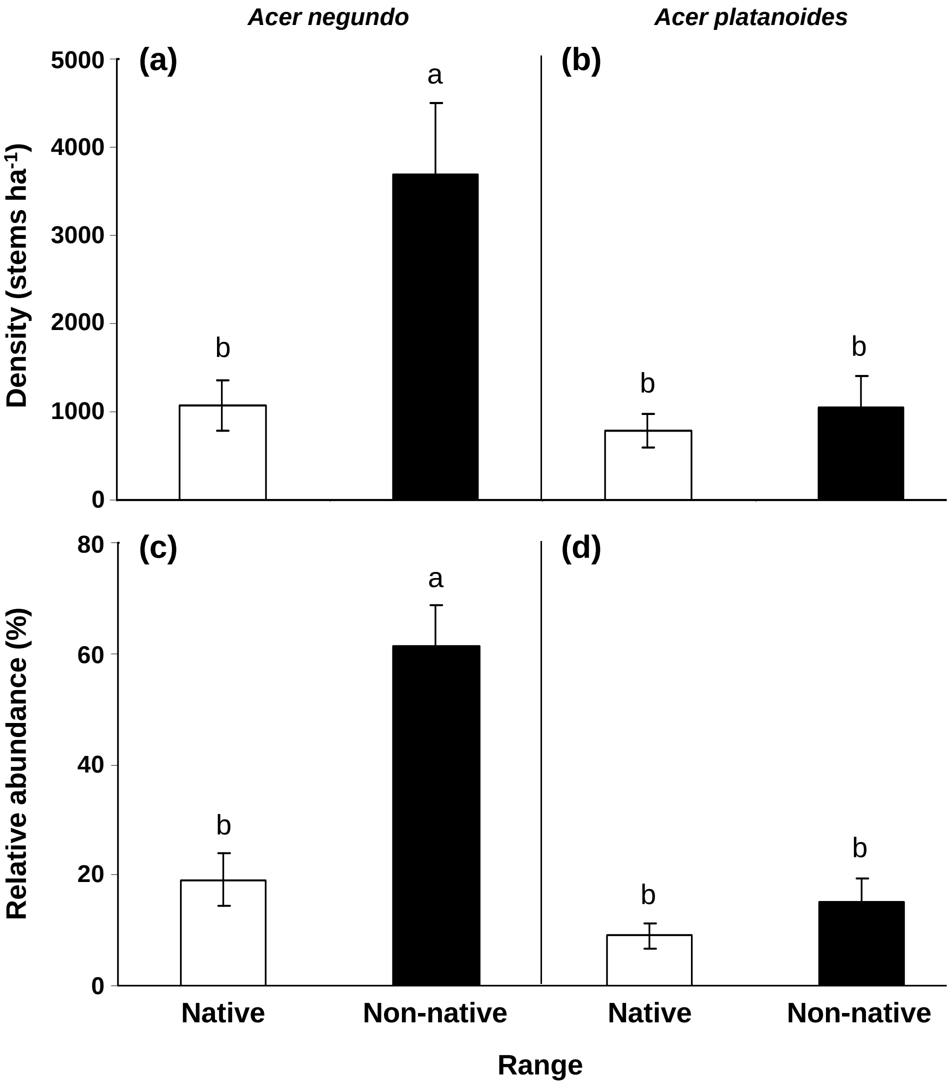

Fig. 1. The density and relative abundance of *Acer negundo* (a, c) and *Acer platanoides* (b, d) populations in their native and non-native ranges. Bars show means ± SE of populations from Southern Ontario, Canada (n = 20) and Southern France (n = 14). *** $p < 0.001$, ** $p < 0.01$.

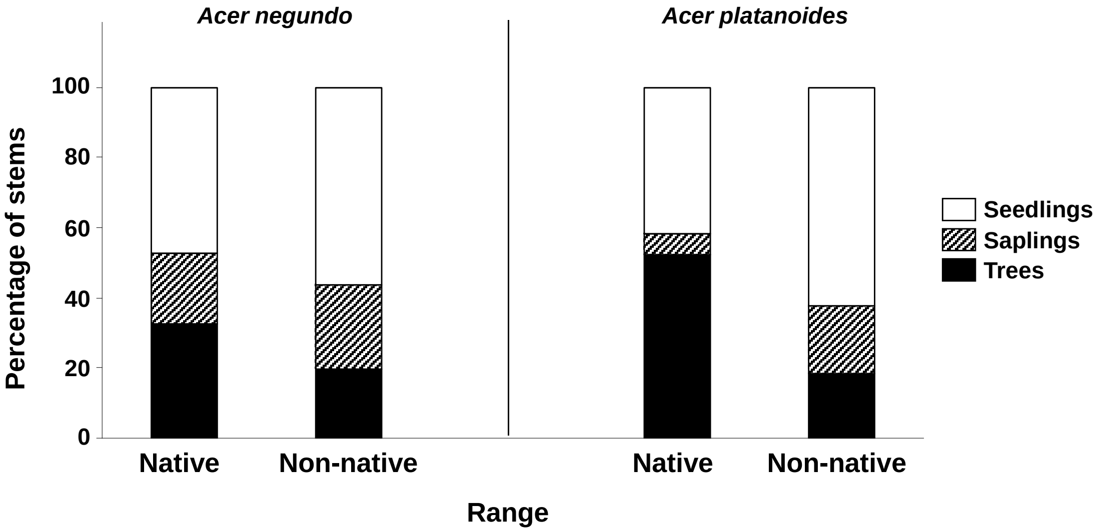

Fig. 2. The age structure of *Acer negundo* and *Acer platanoides* populations in their native and non-native ranges.

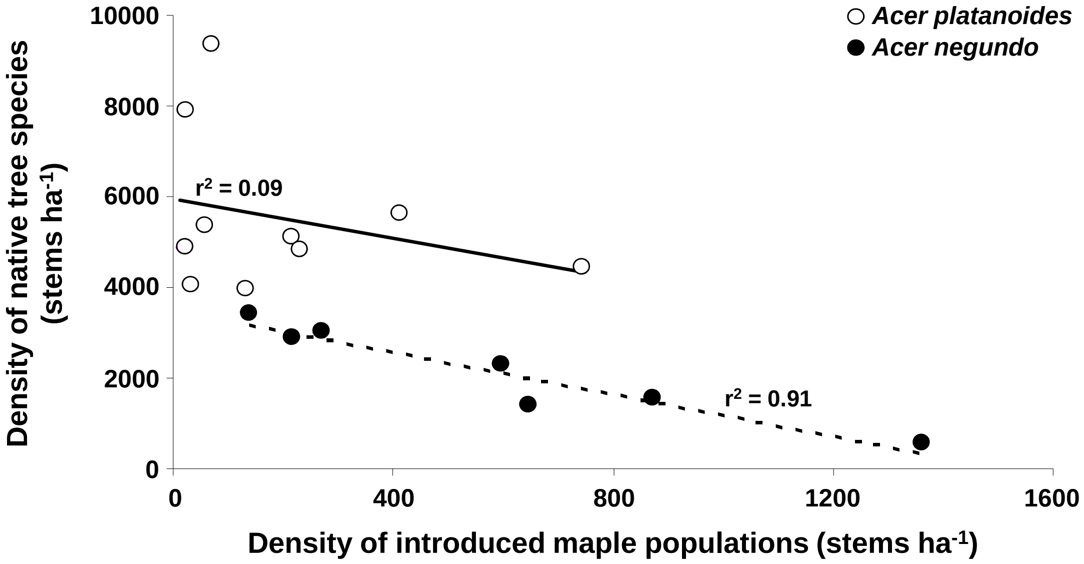

Fig. 3. The relationship between the density of *Acer negundo* and *Acer platanoides* and native tree species of the recipient communities. In Southern France (*Acer negundo* non-native range), n = 7, and n = 10 in Southern Ontario, Canada (*Acer platanoides* non-native range).

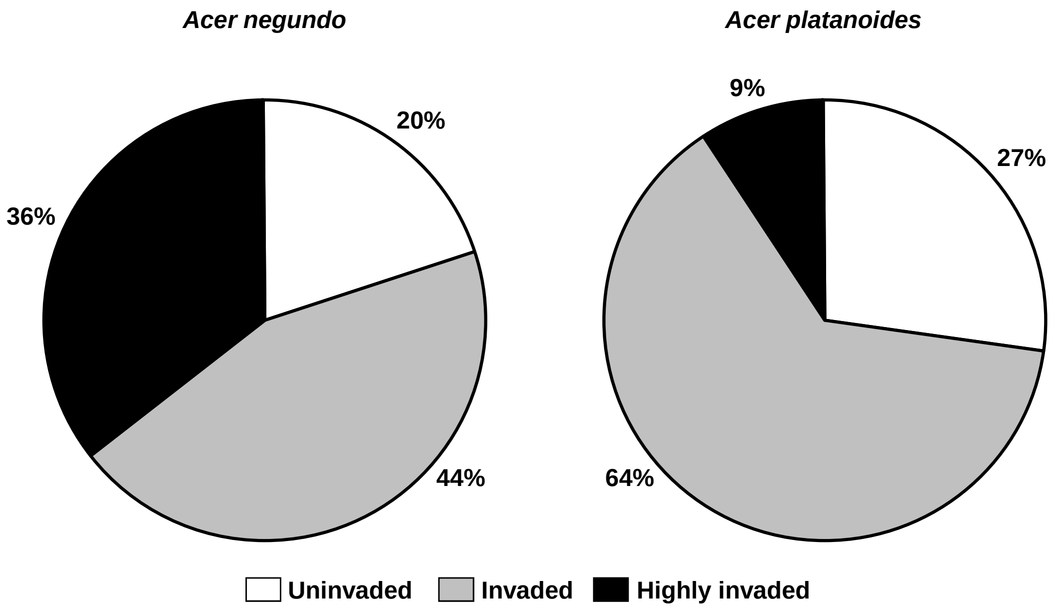

Fig. 4. The regional distribution of *Acer negundo* populations in Southern France and *Acer platanoides* populations in Southern Ontario, Canada. Forests sampled in the non-native range of both species were classified as uninvaded (species absent), invaded (species present with up to 5 individuals, whatever life-stage) or highly invaded (population established with at least 15 adults). A total of 70 and 66 forests were surveyed for presence of *Acer negundo* in Southern France and *Acer platanoides* in Southern Ontario, Canada, respectively.

Chapter 2

A comparison of morphological and physiological traits between one invasive and five co-occurring native tree species

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Abstract

To identify the determinants of invasiveness, comparisons of traits of invasive and native species are commonly performed. Invasiveness is generally linked to higher values of reproductive, physiological and growth-related traits of the invasives relative to the natives in the introduced range. Phenotypic plasticity of these traits has also been cited to increase the success of invasive species but has been little studied in invasive tree species. In a greenhouse experiment, we compared ecophysiological traits between an invasive species to Europe, *Acer negundo*, and early- and late-successional co-occurring native species, under different light, nutrient availability and disturbance regimes. We also compared species of the same species groups *in situ*, in riparian forests. Under non-limiting resources, *A. negundo* seedlings showed higher growth rates than the native species. However, *A. negundo* displayed equivalent or lower photosynthetic capacities and nitrogen content per unit leaf area compared to the native species; these findings were observed both on the seedlings in the greenhouse experiment and on adult trees *in situ*. These physiological traits were mostly conservative along the different light, nutrient and disturbance environments. Overall, under non-limiting light and nutrient conditions, specific leaf area and total leaf area of *A. negundo* were substantially larger. The invasive species presented a higher plasticity in allocation to foliage and therefore in growth with increasing nutrient and light availability relative to the native species. The higher level of plasticity of the invasive species in foliage allocation in response to light and nutrient availability induced a better growth in non-limiting resource environments. These results give us more elements on the invasiveness of *A. negundo* and suggest that such behaviour could explain the ability of *A. negundo* to outperform native tree

species, contributes to its spread in European resource-rich riparian forests and impedes its establishment under closed-canopy hardwood forests.

Introduction

Plant invasions, a main component of global change, are a source of agricultural and economic problems worldwide but also a major ecological threat for biodiversity [1-3], which makes it crucial to understand the key mechanisms that can lead to invasions in an ecosystem. Recent studies concluded that plant invasions are the result of complex interactions between the exotic species performances (i.e., invasiveness), the recipient environment's vulnerability (i.e., invasibility) and the history of the introductions (see for instance [4,5]). With regard to species invasiveness, the success of invasive species seemed to be largely due to their superiority over native species in terms of growth rate and spread into recipient ecosystems; this superiority seemed related to higher values of traits related to fitness such as growth rate, maturity age, fecundity and seed dispersal [4,6-8]. Invasive tree species are doing a lot of damage worldwide [9], and a recent meta-analysis [10] reported that growth rate is a key determinant of the success of invasive tree species. Furthermore, comparative studies that measured native versus invasive tree growth have shown that invasive species are associated with higher growth rates than natives [11-15]. Hence, a reasonable starting point for understanding the dynamics of tree invasion is to precisely quantify growth rate of invasive species in contrast to natives.

In most cases, a higher growth rate results from a more efficient resource use. Major traits related to resource use include leaf traits such as Specific Leaf Area (SLA) or Total Leaf Area (TLA) that serve as a surrogate for light use and carbon assimilation [16] or physiological traits such as photosynthetic rates or nitrogen leaf content [16]. Higher SLA often correlates with a growth advantage for exotic tree species over native ones [13,15,17]. A recent comparison of 29 invasive and non-invasive pine species [18] showed that invasiveness could be predicted by using only species growth rate and SLA. On the other hand, it was also demonstrated that invasive tree species were characterised by higher photosynthetic rates compared to native ones [19,20]. The same conclusion was presented on two species of the genus *Acer* (*A. platanoides* vs. *A. saccharum*, [12]).

However, it is not only their superior morphological or physiological traits that could confer a competitive advantage to invasive species relative to natives but also the dynamic response of their traits [21]. Invasiveness can indeed be related to a higher plasticity of the plant traits in response to environmental changes [22]. Phenotypic plasticity defined as the ability of organisms to alter their morphology and/ or physiology in response to varying environmental conditions has thus been cited to increase the success of invasive species [23-26] since it increases their realised ecological niches. In general, phenotypic plasticity has been applied to the study of plant invasions through the following two distinct hypotheses [27]: (1) invasive species are more plastic than exotic non-invasive species or native species of the recipient communities [28-30] and/ or (2) invasive populations of exotic species have evolved and present a greater plasticity relative to native populations [30-33]. Hence, it is important to compare phenotypic plasticity amongst related pairs of invasive and native species [21] as well as amongst exotic species with different degree of invasive success [26,34,35]. Relative differences in the mean value of traits associated to their plastic response to a range of environmental conditions can provide a powerful tool to explore the invasiveness of exotic species and thus provide mechanistic explanations of invasion events.

To date, most plant invasion studies have focused on herbaceous species. However, although many of the world's most serious invasive plant species are woody species such as several Pine species [36,37], very few studies have explored the link between plasticity and invasiveness in invasive tree species [30,38]. Consequently, empirical studies on tree species are critical to identify the general role of plasticity in explaining invasiveness [21]. Box elder maple (*Acer negundo*) native to North America has been widely planted as an ornamental tree species throughout central and southern Europe. Recently, it has colonised riparian habitats in many regions spreading at the expense of native species and leading to monospecific stands [39-43] in particular in South-Western France [44]. To determine whether resource use efficiency contributes to *A. negundo* invasiveness, we compared its growth and related morphological and physiological traits to that of native co-occurring tree species: *Fraxinus excelsior*, *Fraxinus angustifolia*, *Populus nigra*, *Alnus glutinosa* and *Salix alba*. We used greenhouse treatments spanning different light regimes, soil nutrient resources and disturbance levels. Additionally, adult trees in different riparian forests were compared *in situ* to ensure that results obtained on seedlings under artificial environments were relevant. Specifically, three main questions were addressed here: (i) Are there any growth differences between the invasive *Acer negundo* and native species? (ii) Which traits could best explain the success of the invasive species? (iii) Do the studied species present any plasticity and differences in magnitude of plasticity amongst the environmental conditions?

Material and Methods

Studied species

Native to North America, *Acer negundo* L. is the most widely distributed of all North American maple. *A. negundo* was intentionally introduced in Europe during the seventeenth century (in France around 1749 [64,65]). It is a small to medium sized tree with pinnately compound leaves that usually have five leaflets. First planted in parks, this species is now widely used in South of Europe as an urban tree for avenues for ornamental purposes. The actual distribution area of *A. negundo* in Europe now extends from southern France to Lithuania and from Italy to Germany [66]. In France, its ongoing invasion takes place in the southern two-thirds [67], mainly in riparian habitats. This species is of limited commercial importance and is considered an ecological pest inducing biodiversity losses and river banks instability [68].

At the interface between aquatic and terrestrial ecosystems, riparian forests constitute a key ecosystem that shapes many species' habitats [69] and are particularly vulnerable to invasions [4]. *Acer negundo* mostly invades riparian zones at the ecotone between native softwood and hardwood communities [43,44,70]. In these habitats, five native species can commonly be found in France and thus are likely to compete one or two at a time with *A. negundo*: *Populus nigra*, *Salix alba* and *Alnus glutinosa* are early-successionnal species highly tolerant to disturbances; *Fraxinus excelsior* and *Fraxinus angustifolia* are late-successional and more shade-tolerant species.

Greenhouse experiment design

The objective was to compare the invasive tree species, *A. negundo*, to the four native tree species: *F. excelsior*, *F. angustifolia*, *S. alba* and *P. nigra*. During fall 2003 seeds of *A. negundo* and both *Fraxinus* species were collected *in situ* on populations located along the Garonne River and were sown after vernalization, in spring 2004 at the nursery of the INRA Pierroton research station (44°44'N 0°46'W, west of Bordeaux, Gironde, France). In February 2005, one-year-old seedlings of *S. alba* and *P. nigra* were bought. In March 2005, seedlings of all five species were transplanted in 4 L pots filled with a commercial sphagnum soil mixture (organic matter 80 % of dry matter, pH= 6; Le terreau du producteur, HTA, Saint Cyr en Val, France) and placed in a greenhouse under natural air relative humidity and controlled temperature (day T° 25°C and night T° 15°C). Plants were watered daily to field capacity. The experiment was arranged in a split-split-plot design with complete random blocks (3). The treatments were applied to mimic riparian habitat conditions: shade (3 levels, main plot), nutrient availability (2 levels, sub-plot) and mechanical disturbance (2 levels, sub-sub-plot). Treatments were applied from April 1st 2005, 15 days after leaf unfolding, till June 14th. The shade treatments consisted in a control full light (C, 100% of the ambient radiation), shade (S, 25% of full light) and deep shade (SS, 7% of full light). It was obtained combining thermal cloths over the plants. The nutrition treatment was obtained by providing a complete fertiliser (N+, 4 mg of fertilizer Compo Floranid Permanent, 16% N; 7% P_2O_5; 22.5% SO_3; + metal elements) versus no fertiliser (N-). The fertiliser was applied three times on the 3rd, 14th and 53rd day after the start of the experiment. The fertiliser treatment corresponded to a nutrient level equivalent to that of riparian forest soils in South-

West France [71,72]. Finally, disturbance (D) by river bank flooding was simulated by applying a hand-made partial defoliation (25%, on the 21st and 48th day after the start of the experiment) and compared to non-disturbed (ND) plants. Four individuals per species were randomly assigned to each of the 12 treatments, leading to a total of 720 individuals.

Growth and biomass measurements

At the beginning and at the end of the experiment, total height (cm, ruler, nearest mm, H1 and H2 respectively) was measured on each seedling. The relative height growth rate (RGR_h, mm. $mm^{-1}.d^{-1}$) was calculated for each individual as the difference between the logarithms of final and initial height divided by the number of days between the beginning of the experiment and the harvest:

$$RGR_h = \frac{ln(H_2) - ln(H_1)}{t_2 - t_1} \qquad (1)$$

where $\ln(H_1)$ and $\ln(H_2)$ are the ln-transformed plant heights at the initial (t_1) and final (t_2) time of the experiments respectively [73].

At the end of the experiment, all seedlings were harvested to measure above- and below-ground biomasses (oven-dried at 65°C until constant dry weight) which were used to calculate the root/shoot ratio (RSR, $g.g^{-1}$). Within each treatment and block, 180 plants out of the 720 were sampled randomly but equally amongst the treatments and species to undertake detailed biomass measurements: leaves, stems (branches + stem) and roots were separated. All the leaves were immediately set in distilled water for a minimum of 12h to reach full hydration [74] and total leaf area per individual

(TLA, m^2) was determined then with a planimeter (Light box, Gatehouse, Scientific Instruments LTD, Norfolk, UK). Stem, root and leaf dry weights (oven-dried at 65°C until constant weight) were measured. For each species, specific leaf area (SLA, $m^2.kg^{-1}$) was calculated as the ratio of TLA to leaf dry weight; the leaf weight ratio (LWR, $g.g^{-1}$) as the ratio of leaf dry weight to total individual biomass (stems + leaves + roots).

Photosynthesis and nitrogen content measurements

Gas exchange measurements were carried out in early June, between 8.00 am and 12.00 am, with a steady state through flow chamber (PLC4, PP-Systems, Hitchin, UK) coupled with an infra-red gas analyzer (CIRAS II, PP-Systems, Hitchin, UK). During the measurements, air CO_2 concentration, air temperature and relative humidity (RH) in the chamber were controlled to match ambient air values: 375 ± 3 ppm of CO_2, 25 ± 1°C and 70 ± 10% of RH. All the measurements were made at saturated light (PPFD= 1500 $\mu mol.m^{-2}.s^{-1}$) in order to obtain a light-saturated photosynthetic assimilation rate (A_{max}, $\mu mol\ CO_2.m^{-2}.s^{-1}$) at ambient CO_2. No gas exchange measurements were conducted under the deep shade treatment due to the very low number of leaves per individual. For *Salix alba*, no measurements could be performed either, whatever the treatment, due to a too small leaf size compared to the leaf chamber surface. Three repetitions were made per species and per treatment, leading to a total number of 96 photosynthesis measurements. Light-saturated photosynthetic assimilation rate per unit leaf dry weight (A_{maxw}, $\mu mol\ CO_2.kg^{-1}.s^{-1}$) was calculated as the ratio of A_{max} to SLA.

Leaf nitrogen content was analysed from the leaf samples used for photosynthetic rate measurements (n= 96). Leaf samples were crushed to powder with a ball mill (MM 200, Fisher Bioblock Scientific, France), then nitrogen content (N_m, %) was measured with an elementary analyser Eager 300 CHONS (FlashEA 1112, ThermoElectron Corporation, Waltham, MA, USA). Nitrogen content per leaf area (N_a, g $N.m^{-2}$) was calculated as N_m divided by SLA and the photosynthetic nitrogen use efficiency (PNUE, µmol CO_2.g $N^{-1}.s^{-1}$) as A_{max}/ N_a.

In situ *measurements*

In situ measurements were conducted in May 2006 in four invaded riparian habitats of South-West France. Two sites were located in Cestas along the Eau Bourde River (44°45'20.37''N, 0°40'49.95''W and 44°44'47.00''N, 0°41'17.93''W), one in Bruges along The Jalles River (44°54'12.45''N, 0°36'16.40''W) and one in Saint-Denis-de-Pile along the Isle River (44°59'35.66''N, 0°12'28.45''W). In each site, ten adult individuals from the upper canopy were selected for each species (the invasive species *A. negundo* and the co-occurring native species late-successional *F. excelsior* and early-successional *Alnus glutinosa*). Light-saturated photosynthetic assimilation rate measurements were carried out following the same protocol as for the greenhouse experiment. Leaves used for photosynthesis measurements were collected and their leaf area, dry weight, SLA and nitrogen contents were determined as indicated previously.

Statistical analyses

Statistical analyses were conducted using the SAS software package (SAS 9.1, SAS Institute Inc., Cary, NC). For the controlled conditions experiment, a split-split-plot analysis of variance was performed (proc GLM) and mean differences assessed with SNK and Tukey multiple comparison tests ($\alpha < 5\%$). Main plot (shade) and block effects were tested using shade*block as an error term, the sub-plot effects (fertilisation, fertilisation*shade) were tested using block*fertilisation(shade) as an error term and sub-sub-plot effects (disturbance, disturbance*shade, disturbance*fertilisation, disturbance*shade*fertilisation) were tested using the regular error term according to Federer and King [75]. Analysis of variance (proc GLM) and SNK multiple comparison tests ($\alpha < 5\%$) were used to test species differences *in situ*.

Results

Growth rate

Figure 1 presents the relative growth rate responses to light level, nutrient availability and disturbance as applied to the native and invasive tree seedlings. Nutrient availability induced the most significant difference in growth rate whatever the species: the relative height growth rates (RGR_h values) were 3.2 ($p = 0.0013$), 2.0 ($p = 0.0013$) and 1.6 ($p < 0.0001$) times higher in fertilised compared to non-fertilised treatments, for the invasive, late-successional and early-successional species, respectively (Table 1). Disturbance did not induce any significant difference in growth rate whatever the species and whatever the shade or fertilisation levels. On the other hand, the response to light varied amongst species. There was no significant effect of the shade treatment on the RGR_h of neither group of native species. On the contrary, the shade treatment ($p = 0.0116$) and the interaction shade*fertilisation ($p = 0.0155$) had a significant impact on the relative growth rate of the invasive species. Under fertilised and full light conditions, *A. negundo* and early-successional native species displayed significantly higher RGR_h than late-successional native species (with 50 to 110% increases according to the treatment); in constrast, under fertilised and deep shade conditions, *A. negundo* presented dramatically lowered growth rates relative to the early-successional species. To sum up, the growth rate plasticity in response to resource (light x nutrient) availability was 9.6 times higher in *A. negundo* seedlings relative to the native seedlings: *A. negundo* growth rate was 13 times higher in full light and shade (on average) compared to the deep shade level (Fig. 1) under high nutrient availability, whereas the same environmental changes only resulted in a 1.23 and 1.5 time increase in RGR_h for the early- and late-successional native species, respectively.

Biomass allocation and specific leaf area

Overall, nutrient availability was the main factor affecting biomass allocation, the response to light availability being trait and species dependent. Allocation to roots was significantly lower under the fertilised treatments (Table 1), with a 1.8, 1.2 and 1.6 reduction for the invasive, early- and late-successional species, respectively. The LWR increased with fertilisation for all species (Fig. 2). However, for the invasive species, responses to fertilisation in allocation towards foliage were primarily significant under the fertilised full light and shade treatments only (significant shade*fertilisation $p = 0.0213$ on LWR, Table 1). TLA was significantly increased by fertilisation for all species (Table 1): for the invasive, TLA was 3.7 times higher compared to non-fertilised treatments, vs. only 2.1 and 2.3 times higher for the early- and late-successional species. The invasive species displayed a lower RSR than the native species under fertilised conditions whatever the light treatment ($0.01 < p < 0.05$, Fig. 2). Late-successional native species presented the highest allocation to roots and significant differences in allocation to roots in response to light availability (shade $p = 0.0148$, shade*fertilisation $p = 0.0161$, Table 1, Fig. 2) with a fertilisation interaction. The invasive species also presented a higher allocation to leaves than the native species across all treatments ($0.0003 < p < 0.02$; +170 and +74% increase in mean LWR, compared to the native early- and late-successional species, respectively). Under fertilisation and full light or shade conditions, the TLA of the invasive species reached three-fold higher values than either early- and late-successional species ($p < 0.01$), similarly to that observed for relative growth rate and allocation to foliage (Fig. 2).

All the species in the greenhouse experiment presented significantly lower SLA under increased light regimes ($p < 0.001$, Table 1), whereas fertilisation and disturbance had no effect. Furthermore, the invasive species seedlings exhibited higher SLA than the native ones, SLA values being 1.6 and 1.3 times higher on average for the invasive species compared to the early- and late-successional species, respectively (Fig. 2; see Appendix 11 for means per experimental conditions). *In situ* measurements on adult trees (Fig. 3) indicated similar differences between species groups ($p < 0.001$), with higher SLA values for the invasive species compared to the native early- and late-successional ones (ratio 1.7 and 1.4, respectively; Appendix 11).

Physiological traits

The same physiological traits – photosynthetic assimilation rate, leaf nitrogen content and photosynthetic nitrogen use efficiency - were measured on seedlings in the greenhouse (Fig. 4) and on adult trees in the field (Fig. 3). A_{max} and A_{maxw} were quite conservative over the different environments for all species, with no significant differences according to the shade, fertilisation or disturbance treatments (except a fertilisation effect for the late-successional native species, Table 1). The leaf nitrogen contents (N_m, %) significantly increased with fertilisation, whatever the light availability and disturbance regime. The pattern observed in the response of nitrogen content on a leaf area basis (N_a) to shade and fertilisation was similar for all species: N_a significantly increased with fertilisation in interaction with the shade treatment, the nitrogen content being on average three times higher under full light * fertilisation treatment (Table 1, Fig. 4), compared to the other modalities. Overall, the treatments had no significant effects on PNUE (Table 1).

The invasive tree species had significantly lower photosynthetic capacities (A_{max}, A_{maxw}) than both the native early- and late-successional species which performed equally. *In situ*, the light saturated assimilation rate of the invasive species equalled half that of the natives. The differences observed on the seedlings were quite similar, the early-successional species presenting the highest photosynthetic rates (species group effect: $0.01 < p < 0.04$), from 1.5 to 5.7 time increase, according to the treatment; the invasive species performed equally to the late-successional natives (Fig. 4). No difference was found between species in leaf nitrogen content expressed on a biomass basis (N_m, Fig. 4) whereas N_a of the early-successional species was significantly higher compared to that of the late-successional and the invasive species ($0.003 < p < 0.05$, according to the treatment). In the field on adult trees, stronger differences were found, with both early- and late-successional species presenting higher nitrogen contents than the invasive species ($p < 0.001$; 70% more compared to the natives, Fig. 3). On adult trees *in situ*, PNUE demonstrated the lower efficiency of the invasive species compared to the natives ($p = 0.002$, Fig. 3); in the greenhouse, the photosynthetic nitrogen use efficiency was not significantly different between the species (Fig. 4).

Discussion

In the present study, we compared the growth, physiology and allocation patterns of an invasive tree species, *A. negundo,* to co-occurring native tree species across a wide range of controlled environmental conditions including light, nutrient availability and disturbance using 1 year-old seedlings under greenhouse conditions and adult trees in the field. Overall, *A. negundo* seedlings grew better under high-level resource environments (full light and fertilised). The relative success of *A. negundo* was, however, not related to any physiological advantage *per se* but to its higher plasticity in allocation to foliage in response to increasing nutrients and light.

Functional strategies

We showed that under high resource environments, the invasive *A. negundo* exhibited higher growth than the co-occurring native tree species. This finding is consistent with a large majority of studies conducted on woody species wherein invasives outcompeted natives in the field [11,13,15,18,19] or in experimental plots [14,45,46]. Using a transplant design in the field, Saccone et al. [43] showed that *A.*

negundo could outcompete native species through a trade-off between high survival in shaded environments and high growth under full light conditions. For species of the same genus *Acer*, Kloeppel and Abrams [12] demonstrated that the height growth increment of the native *A. saccharum* was more than two times lower than the growth rate of the invasive *A. platanoides*.

In our study, the growth success of the invasive tree was not related to any physiological advantage over its native counterparts. On the contrary, both in the field for adult trees and under all light and nutrient controlled conditions for seedlings, *A. negundo* photosynthetic rates and leaf nitrogen contents (N_a, N_m) were lower or equivalent to those measured on the late and early-successional native species. Several studies reported equivalent photosynthetic rates or characteristics (V_{cmax}, J_{max}, Fv/Fm) when comparing invasive and native tree species [15,18,20] or shrubs [47]. In some studies, a physiological advantage was even demonstrated in favour of the invasives [12,19,48]. No previous study on woody plants demonstated a physiological inferiority of the invasive species. In the literature regarding the nitrogen leaf content and nitrogen use efficiency, most studies concluded to a superiority of invasive tree species [13,15,20,49-51] and some to an absence of differences [12,47]. Again no similar study involving tree species ever demonstrated a net and significant physiological disadvantage related to nitrogen content of the invasive tree compared to its local native competitors. Thus although we have been working on seedlings, the findings of our study are novel for they represent the first study on woody plants to our knowledge that demonstrated that the growth superiority of an invasive tree was associated to a physiological disadvantage relative to the natives; such a paradox has only been observed one time out of four on herbaceous species (review by [25]).

The specific allometric properties of *A. negundo* clearly demonstrated that despite its poor physiological performances, it could outcompete local species growth due to a large investment in the development of aerial structures (lower RSR, higher LWR and TLA, higher SLA) thus maximising solar radiation capture. Under controlled conditions, its total leaf area can represent up to three times that of the native seedlings, its leaf weight representing 20 to 40% of its total biomass, in opposition with the compared natives (5-20%). Large relative investment in foliage of invasive species compared to co-occurring natives was commonly observed [15,18,52,53]. However few studies really measured the biomass repartition between compartments of invasive tree species and SLA was more largely measured in trees as a proxy to detect higher light resource capture capacities. The higher SLA values that we observed in *A. negundo* were in accordance with many studies covering more than 50 species of woody invasives [13,15,18,47,49,50,53,54].

Our study also generally supports the conclusions of a recent synthesis comparing 34 woody species in Argentina, including the invasive *A. negundo* [54], which found that large leaf and foliage trait values (SLA and TLA) can be common characteristics to woody invasive species; but contrary to our conclusion, they also emphasized a physiological superiority as an explanation for invasiveness. Hence, this synthesis concluded that invasive and native woody species differ in functional strategies. Another synthesis recently published using the relationships between structural (SLA) and physiological trait values (A_{max}, N content) concluded that native and invasive species (122 species in Australia) use similar strategies for light capture and carbon assimilation [55]; the success of invasive species was thus generated by their positions at the higher end of the range of species traits values. Similarly, Thompson and Davis [56] proposed to use a continuous scale of traits to compare species from "loser" to "winner" species; *A. negundo* would then be identified as a "winner" species. However, our results do not support these hypotheses since the native species physiological characteristics largely exceeded those of the invasive, whereas *A. negundo* clearly demonstrated a specific strategy of massive investment in leaf foliage, which largely compensated for its lower photosynthetic rates and nitrogen use efficiency. This strategy can explain its elevated growth rates under high resource environments and its invasiveness in riparian habitats.

Magnitude of plasticity

Our experiment demonstrated that *A. negundo* is highly plastic in growth and traits such as TLA or LWR in response to changes in nutrient availability and light levels. *A. negundo* seedlings performed poorly relative to natives under low nutrient conditions whatever the light regime and under fertilised but light-limited environments. *A. negundo* also strongly benefited from increases in light and nutrients whereas native species plasticity remained limited. Indeed, it seems that the success of invaders relative to local species is highly dependent on the growing conditions [25], as the native species would stand up to the competition impeding invasion success under stressful environments (low nutrient, water or light availability). In accordance with our results, several studies also showed a pattern of superior allocation plasticity in invasive species and a massive investment to foliage in response to resource enrichment [8,15,21,50,52,53,57]. Very few studies examined the physiological-trait plasticity in invasive tree species. Nonetheless, three studies have found a higher plasticity in photosynthetic characteristics [19,21] and nitrogen content [50] in the natives with increasing resources compared to the invasives, while several others found a higher plasticity of invasive woody species in growth responses to nitrogen and/or light compared to the natives [14,19,46,49,58,59]. A recent experiment comparing invasive and native vines [53] concluded to the superior plasticity of the invasives in traits related to growth and allocation (LWR, SLA) and not in physiological traits (A_{max}, WUE), in response to light availability, which is in total accordance with our conclusions. So both responses can occur in invaded forests, higher or lower plasticity of the invasive species, likely depending on the particular species and the characteristics of the invaded system. Our study forms a first comparison of native and invasive tree species that covers both field and controlled resource conditions, investigating physiology and allometry, which allowed us to increase our knowledge regarding the mechanisms of invasiveness of *A. negundo.*

In the conceptual framework of Richards's theory of plasticity [27] three strategies were proposed by which invaders can outcompete native species. (i) Jack-of-all-trade, the invader having superior abilities across stressful environments, (ii) Master-of-some, the invader being able to outcompete its counterparts under favourable conditions only and (iii) Jack-and-master a combination of both strategies. Our results clearly show that *A. negundo* has a master-of-some strategy that can explain the secret of its success at least in the riparian forests. Higher plasticity in allocation traits can allow *A. negundo* individuals to rapidly benefit from changes in their environmental conditions (nutrient availability, light) thereby capitalising on the fluctuating resources of these specific riparian ecosystems to overgrow local species. Thus, in the actual context of increasing nitrogen deposition [60], the spread of *A. negundo* could be accentuated due to both its greater performance under high nutrient availability and to its higher plasticity relative to native species. Dramatic impacts of nitrogen deposition on forest functioning have indeed been demonstrated, particularly the increase of the annual rate of biomass increment [61] and the facilitation of invasions [62].

Conclusions

Our study added to the general debate on the mechanisms and species traits that explain the success of invasive tree species over their native counterparts. The success of *A. negundo* as an invasive species is likely to be driven by its superior growth ability compared to native species in resource-rich environments (light, nitrogen), due to a higher plasticity in biomass allocation. Moreover, two further steps would be particularly relevant to determine: (i) whether the higher magnitude of plasticity is adaptive by relating trait values to fitness proxies under different environments [59] and (ii) whether the invasive populations present genetic differentiation in the plasticity of their traits [10,63] by comparing populations from both the native and invasive ranges.

High plasticity in biomass allocation could be a key to understanding tree species invasiveness; the plastic response of *A. negundo* could impede its establishment under closed-canopy hardwood forests while its high plasticity would perfect its growth and potentially allow its spread in resource-rich riparian forests down to the river.

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Table 1. Split-split-plot analysis of variance of tested environmental conditions for measured traits and group of species.

Variables	Species	Shade	Fertilization	Disturbance	S x F	S x D	F x D
RGR_h	Invasive	**0.012**	**0.001**	0.471	**0.016**	0.964	0.334
	Early sc.	0.169	**<0.001**	0.447	0.312	0.610	0.204
	Late sc.	0.504	**0.001**	0.528	0.085	0.834	0.593
RSR	Invasive	0.161	**<0.001**	**0.012**	0.390	0.186	0.178
	Early sc.	0. 962	**0.018**	0.762	0.461	0.588	0.097
	Late sc.	**0. 015**	**<0.001**	0.066	**0. 016**	0.680	0.849
TLA	Invasive	0.065	**0.007**	**0.017**	0.084	0.559	0.215
	Early sc.	0.156	**0.001**	0.297	0.067	0.770	0.898
	Late sc.	**0.017**	**0.001**	**<0.001**	**0.021**	0.127	0.099
SLA	Invasive	**<0.001**	0.168	0.115	0.249	**0.023**	**<0.001**
	Early sc.	**<0.001**	**0.020**	0.253	0.976	0.720	0.776
	Late sc.	**0.001**	0.052	0.655	0.165	0.988	0.593
LWR	Invasive	**0.012**	**<0.001**	**<0.001**	**0.021**	0.383	0.965
	Early sc.	0.184	**<0.001**	0.077	0.268	0.965	0.801
	Late sc.	0.437	**<0.001**	**<0.001**	**0.034**	0.784	0.349
A_{max}	Invasive	0.710	0.043	0.168	0.450	0.897	0.986
	Early sc.	0.110	0.407	**0.041**	0.600	0.573	0.417
	Late sc.	0.588	**0.005**	**0.008**	0.055	0.243	0.553
A_{maxw}	Invasive	**0.023**	0.086	0.130	0.242	0.541	0.752
	Early sc.	**0.002**	0.800	0.512	0.771	0.986	0.947
	Late sc.	0.098	**0.004**	0.095	**0.013**	0.457	0.243
N_m	Invasive	0.836	**<0.001**	**0.012**	**0.008**	0.219	0.141
	Early sc.	0.603	**<0.001**	0.459	**0.002**	0.101	0.371
	Late sc.	**0.037**	**<0.001**	0.972	**<0.001**	0.773	0.548
PNUE	Invasive	0.253	0.213	0.171	0.398	0.048	0.107
	Early sc.	0.629	0.090	**0.029**	0.257	0.634	0.213
	Late sc.	0.056	**0.037**	**0.023**	0.120	0.777	0.426
N_a	Invasive	**<0.001**	**0.006**	**0.018**	**0.007**	0.445	0.957
	Early sc.	**<0.001**	**<0.001**	0.479	**<0.001**	**0.028**	0.374
	Late sc.	**<0.001**	**<0.001**	0.872	**<0.001**	0.812	0.654

Significant p values ($p < 0.05$) are presented in bold. Species are grouped by strategy: the invasive species is *Acer negundo*, early-successional native species are *Salix alba* and *Populus nigra* and late-successional native species are *Fraxinus excelsior* and *Fraxinus angustifolia*. Traits are: RGR_h relative growth rate in seedling height, RSR root/shoot ratio, TLA total leaf area, SLA specific leaf area, LWR leaf weight ratio, A_{max} light-saturated assimilation rate per unit leaf area, A_{maxw} light-saturated assimilation rate per unit leaf dry weight, N_m nitrogen content, N_a nitrogen content per unit leaf area and PNUE the photosynthetic nitrogen use efficiency.

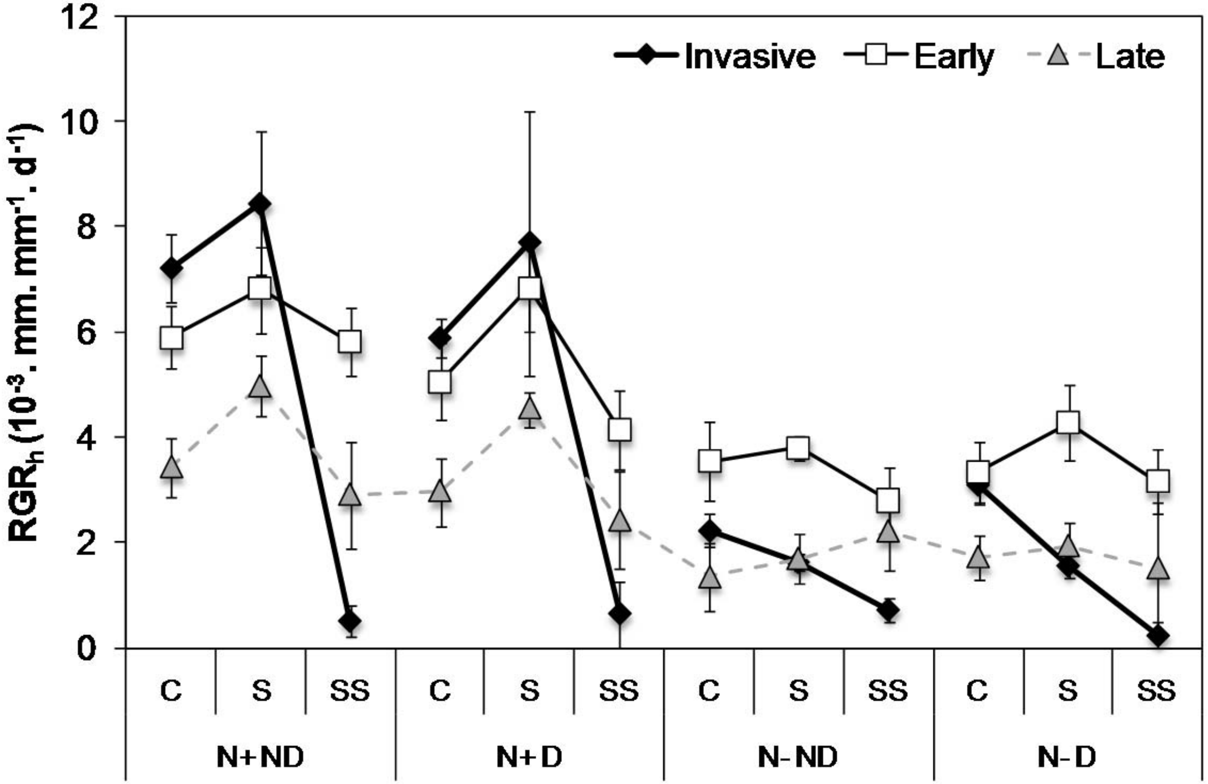

Fig. 1. Relative height growth rates (RGR$_h$, mm. mm^{-1}. d^{-1}. 10^{-3}) of the invasive and native species according to the environmental conditions. Values are means of nine to twelve seedlings (± 1 SE of the mean) for the invasive species (*Acer negundo*, full diamonds), late-successional native species (*Fraxinus excelsior* and *Fraxinus angustifolia*, grey triangles) and early-successional native species (*Salix alba* and *Pinus nigra*, open squares) across the three shade levels (Full light C, Shade S, Deep shade SS), the two nutrient levels (nutrient supply N+ vs. no supply N-) and the two disturbance regimes (Disturbed D vs. Non-disturbed ND).

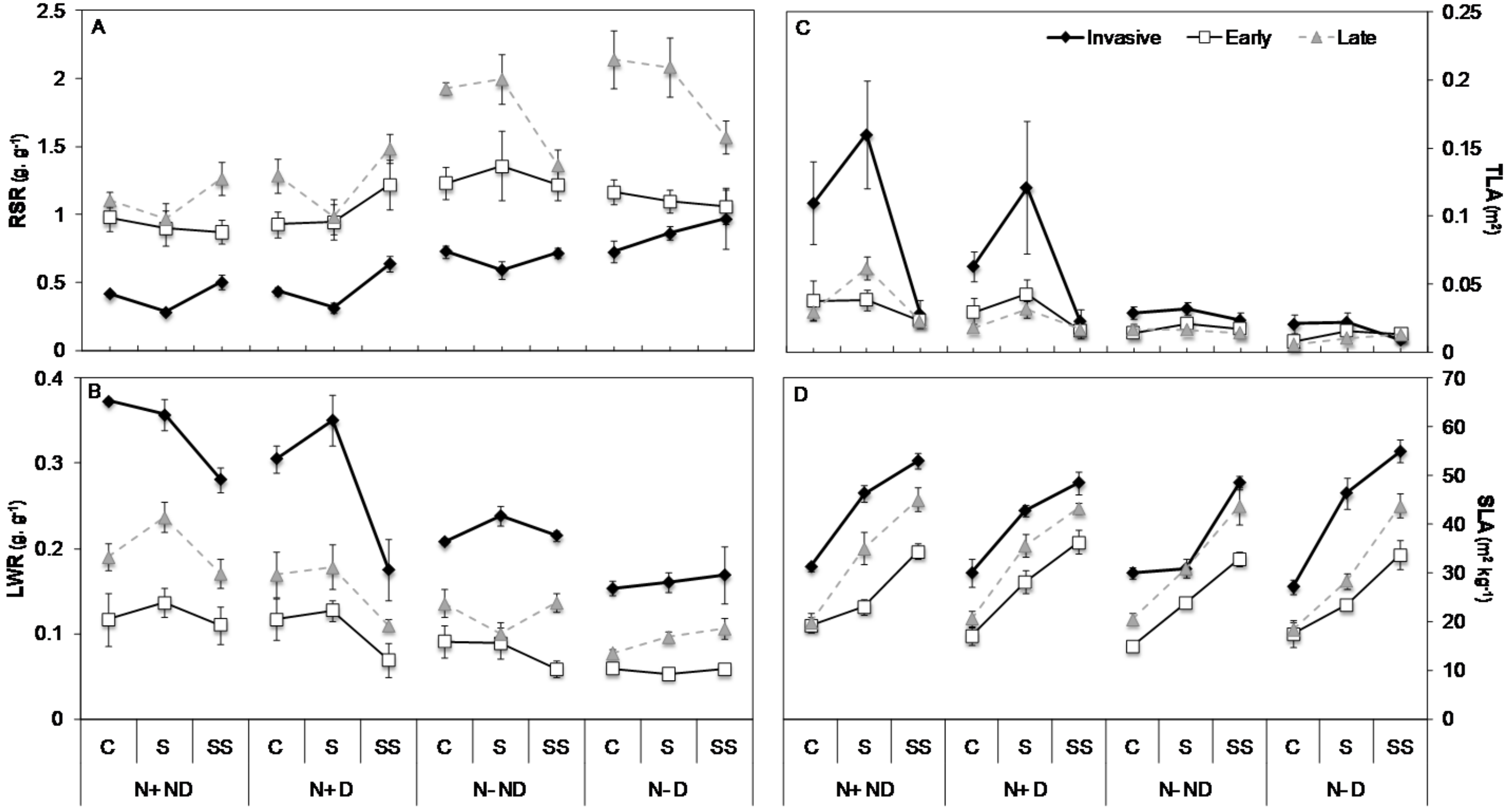

Fig. 2. (A) Root/shoot ratio (RSR), (B) leaf weight ratio (LWR, g. g^{-1}), (C) total leaf area (TLA, m²) and (D) specific leaf area (SLA, m². kg^{-1}) of the invasive and native species according to the environmental conditions. Values are means of nine to twelve seedlings (± 1 SE of the mean) for the invasive species (*Acer negundo*, full diamonds), late-successional native species (*Fraxinus excelsior* and *Fraxinus angustifolia*, grey triangles) and early-successional native species (*Salix alba* and *Pinus nigra*, open squares) across the three shade levels (Full light C, Shade S, Deep shade SS), the two nutrient levels (nutrient supply N+ vs. no supply N-) and the two disturbance regimes (Disturbed D vs. Non-disturbed ND).

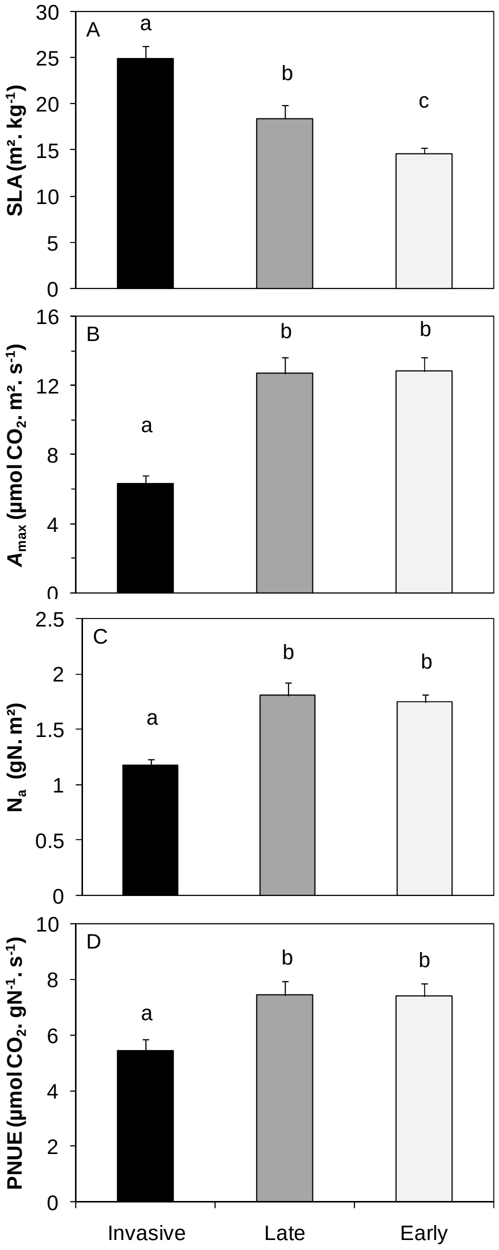

Fig. 3. (A) Specific leaf area (SLA, m². kg^{-1}), (B) light-saturated assimilation rate (A_{max}, µmol CO_2. m^{-2}. s^{-1}), (C) leaf nitrogen content (N_a, g. m^{-2}) and (D) photosynthetic nitrogen use efficiency (PNUE, µmol CO_2. g^{-1} N. s^{-1}) of the invasive species (*Acer negundo*, full bars), the late-successional native species (*Fraxinus excelsior*, grey bars) and the early-successional native species (*Alnus glutinosa*, light-grey bars) as measured *in situ*. Values are means of 25 to 34 adult trees (± 1 SE of the mean). ANOVA were highly significant for all variables, respectively: F= 18.51 $p < 0.0001$; F= 26.85 $p < 0.0001$; F= 19.6 $p < 0.0001$; F= 6.96 p= 0.0016. Means with the same letters are not significantly different (at p = 0.05).

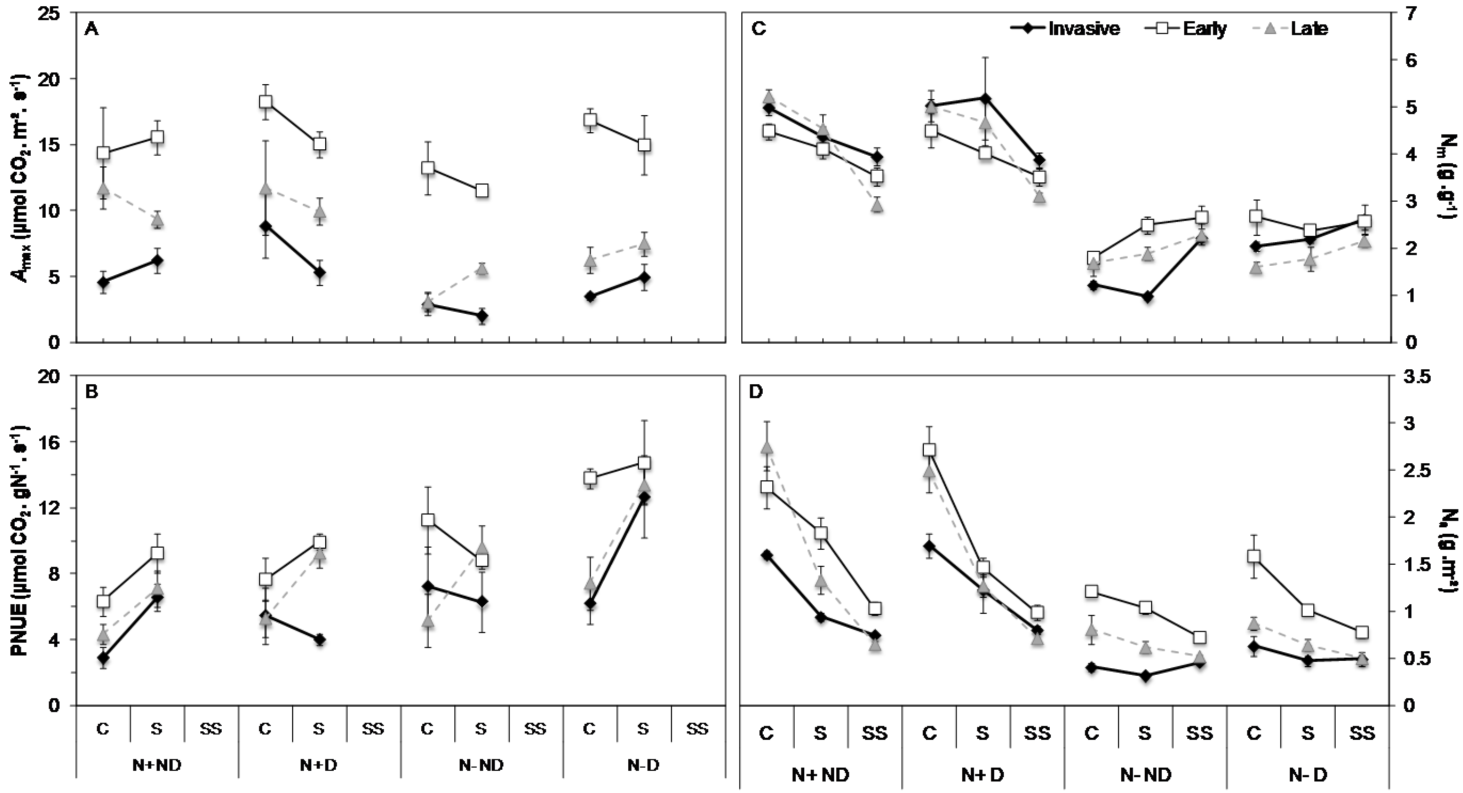

Fig. 4. (A) Light-saturated assimilation rate (A_{max}, µmol CO_2. m^{-2}. s^{-1}), (B) photosynthetic nitrogen use efficiency (PNUE, µmol CO_2. g^{-1}N. s^{-1}) and (C, D) leaf nitrogen contents (N_m % and N_a g. m^{-2}) of the invasive and native species according to the environmental conditions. Values are means of nine to twelve seedlings (± 1 SE of the mean) for the invasive species (*Acer negundo*, full diamonds), late-successional native species (*Fraxinus excelsior* and *Fraxinus angustifolia*, grey triangles) and early-successional native species (*Salix alba* and *Pinus nigra*, open squares) across the three shade levels (Full light C, Shade S, Deep shade SS), the two nutrient levels (nutrient supply N+ vs. no supply N-) and the two disturbance regimes (Disturbed D vs. Non-disturbed ND).

Chapter 3

A systematic review and meta-analyses on tree invasions

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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.

Key words

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, 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; 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 *(i)* if its entry in the community is facilitated by native species (theory of facilitation; Bruno et al. 2003), *(ii)* if natural or anthropogenic disturbances affect the community (disturbance hypothesis; Mack et al. 2000) or *(iii)* 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 defence 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 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 & Jeschke 2009). We included in this study tree species only, defined as in Richardson & Rejmanek (2011, *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.

Material 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 (Appendix 12). 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).

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 (*i*) between native and invasive populations of the invasive tree species studied or (*ii*) between native species of the introduced range and the invasive tree species (Appendix 13). 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 6308 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 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 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 (Appendix 14). 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. 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 ($d_{EICA} = 0.6469$, $\mathrm{d}_D = 0.5647$, $d_{FRA} = 0.4654$ 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 ($Q_{between} = 5.32$, $df = 5$, $P = 0.38$).

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 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 five 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; Dezotti 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 and Smith 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; Siemann and Rogers

2007; Zou et al. 2008a; Zou et al. 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. 2005), 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; Reinhart et al. 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 & Rejmanek, *in press*).

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Table 1. List of articles that effectively tested one of the eight dominant invasion hypotheses on invasive tree species. For each study, were respectively reported the invasive tree species studied, the study location, the hypothesis tested and the functional traits measured.

Reference	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 x 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	-
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
Nuñez 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	-
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

‡ Studies included in the meta-analysis conducted on hypotheses. § Studies included in the meta-analysis conducted on functional traits. [a] 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. [b] B: Biomass, Ge: Germination, Gr: Growth rate, DC: Density/ Cover, S: Survival.

Table 2. Systematic review based on eight dominant hypotheses proposed to explain the success of invasive species. 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 14 for more information on the invasive tree species studied.

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 Nötzold (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

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.

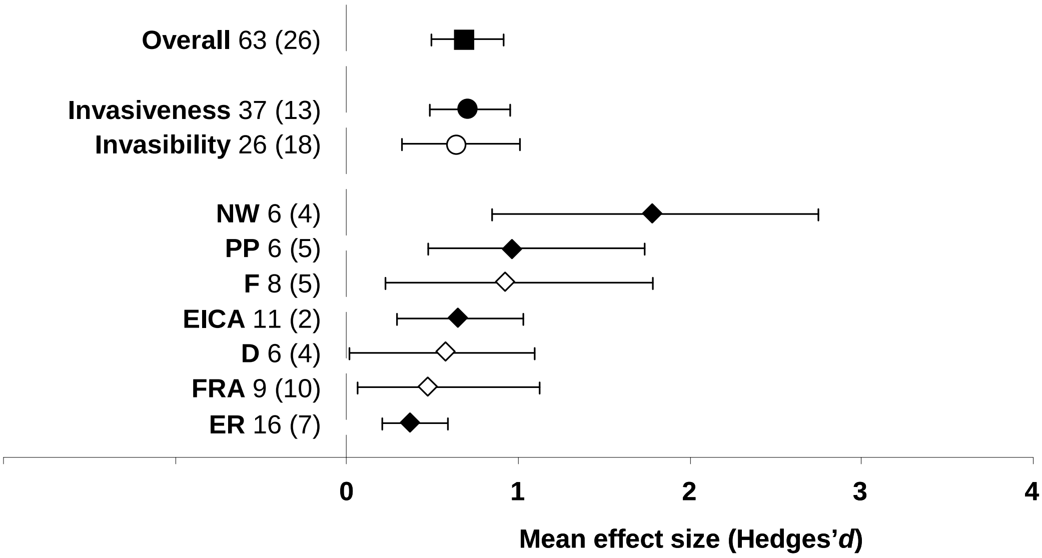

Fig. 1. Weighted-mean effect sizes (Hedges' *d*) and 95% bias-corrected confidence intervals calculated for seven dominant hypotheses proposed to explain invasion in trees (the effect size could not be calculated for the empty niche hypothesis). The number of studies and, in parentheses, the number of 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.

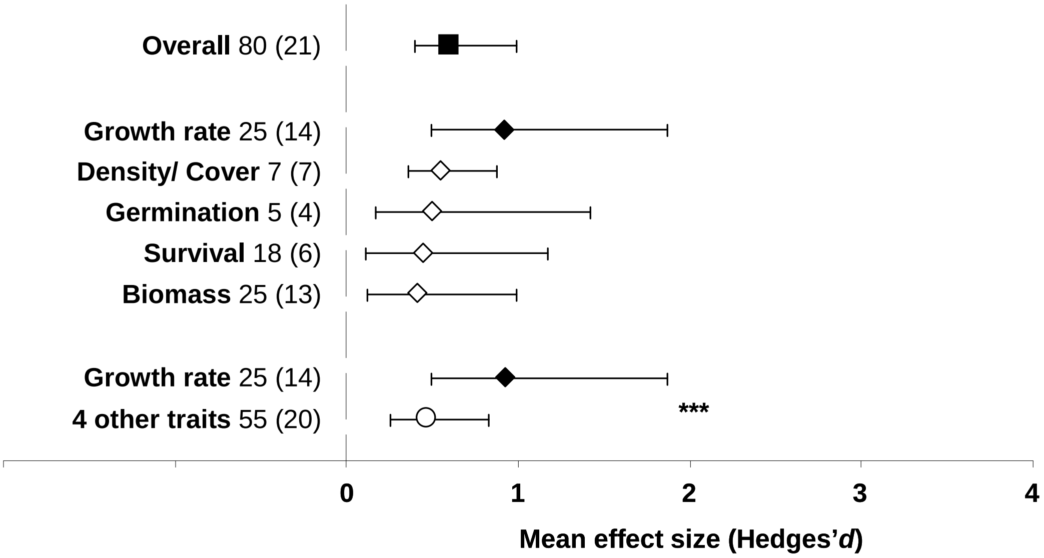

Fig. 2. Weighted-mean effect sizes (Hedges' *d*) and 95% bias-corrected confidence intervals calculated for the five main functional traits used in invasive tree species. The number of studies and, in parentheses, the number of invasive tree species they refer to, are given on the left-hand side of the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

Chapter 4

Assessing genetic adaptation and phenotypic plasticity in two invasive maple trees

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Magnitude of genetic differentiation and phenotypic plasticity in life-history traits between native and introduced range populations of invasive maple trees.

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Abstract

Despite a growing body of literature indicating evolutionary changes in non-native ranges of exotic plants and the major concern that currently represent aggressive tree species, information is still scarce about the evolutionary ecology of invasive trees.

Methods: Using two reciprocal common gardens in the native and introduced ranges of each species, we compared native and invasive populations of both *Acer negundo* and *Acer platanoides*. Almost 3000 seedlings were planted in Canada and in France and various life-history traits related to growth, phenology, physiology and morphology were monitored over four years. Within common gardens, invasive populations of *A. negundo* genetically differed from their native conspecifics in all the traits examined. They were larger than native populations in the introduced range but had lower survival and reduced photosynthetic capacity in both gardens. In addition, between gardens, invasive genotypes expressed greater phenotypic plasticity for growth and leaf phenology. In contrast, native and invasive populations of *A. platanoides* did not show genetic differentiation for any traits across gardens nor differ in plasticity. While we did not detect evidence of an evolutionary change for *A. platanoides*, both genetic changes and phenotypic plasticity are involved in *A. negundo* invasiveness.

Key words

Acer negundo, *Acer platanoides*, evolutionary change, genetic divergence, invasion, phenotypic plasticity, reciprocal common gardens

Introduction

Biological invasions provide a tremendous opportunity to study species' adaptive evolution in response to environmental changes (Maron et al. 2004b; Urbanski et al. 2012). Because exotic species have to cope with new conditions before being able to invade non-native areas (Allendorf and Lundquist 2003), evolutionary processes such as genetic drift events (*i.e.* founder effects and bottlenecks), hybridization between species or disparate source populations and novel selection pressures are expected to play a major role in plant invasion (Ellstrand and Schierenbeck 2000; Lee 2002). In particular, selection can improve competitive ability in response to lower levels of abiotic stress (Alpert et al. 2000) and release from natural enemies (Evolution of Increased Competitive Ability (EICA) hypothesis, Blossey and Nötzold 1995).

For decades, life-history traits have been studied as major determinants of plant invasiveness (Hawkes 2007; van Kleunen et al. 2010). For instance, growth rate has often been successfully tested as a key factor promoting plant invasion (Pattison et al. 1998; Erfmeier and Bruelheide 2004; Lamarque et al. 2011). Traits related to physiology and leaf morphology are important determinants of growth rate (Grotkopp et al. 2002; Wright et al. 2004) and higher values in favour of invasive species have long been reported in the literature for these traits (Kloeppel and Abrams 1995; Pattison et al. 1998; Nagel and Griffin 2004). Phenology – the timing of periodic events such as leaf unfolding and flowering – may also contribute to exotic plant invasiveness, particularly through seasonal priority effects and higher phenological plasticity in response to variable environments (Godoy et al. 2009; Wolkovich and Cleland 2011). Overall, any of these traits that are beneficial under novel environmental conditions are subjected to evolutionary processes (Bossdorf et al. 2005). Consequently, invasive populations of exotic species have been found to undergo evolutionary changes in a variety of traits related to dispersal ability (Cheptou et al. 2008), reproduction (Ridley and Ellstrand 2009), defense (Maron et al. 2004a; Rapo et al. 2010), growth (Siemann and Rogers 2001; Huang et al. 2010; Hodgins and Rieseberg 2011) and leaf physiology and morphology (Buswell et al. 2011; Feng et al. 2011). Similarly, they are also able to evolve greater phenotypic plasticity compared to populations from the native range if more plasticity offers a fitness advantage in the novel environments (Leger and Rice 2003; Richards et al. 2006; Lavergne and Molofsky 2007; Zou et al. 2009).

Quantifying evolutionary changes and in particular determining genetically-based phenotypic differentiation between populations requires the use of the classical common garden approach (Connor and Hartl 2004; Vitasse et al. 2009a). Although this is not a general feature for all invaders (Franks et al. 2008a; Cripps et al. 2009; Andonian and Hierro 2011), many studies that compared functional traits between native and invasive populations of exotic species in common environments found support for genetically-based differences in phenotype between populations (Siemann and Rogers 2001; Leger and Rice 2003; Maron et al. 2004a; Genton et al. 2005; Zou et al. 2007; Feng et al. 2011). For instance, Blumenthal and Hufbauer (2007) found a consistent pattern of increased size in introduced populations of 14 invasive species. Nonetheless, a challenge in analysing the results of such experiments is that most of them are conducted in only one garden, leading to problems in interpretation when genotype-environment interactions occur (Williams et al. 2008; Flory et al. 2011b). Therefore, multiple common garden experiments are required in both native and introduced ranges (Willis and Blossey 1999; Bossdorf et al. 2005; Ebeling et al. 2011).

Genetic differentiation and phenotypic plasticity were contrasted between native and invasive populations of two maple tree species using reciprocal common gardens to examine the relative importance of plasticity versus adaptation. The species *A. negundo* and *A. platanoides* are aggressive invaders into deciduous forests of the Northern Hemisphere. We hypothesized that populations from native and non-native ranges would express genetically based changes in phenotype within common gardens. Specifically, we predicted that, relative to native conspecifics, invasive populations would (i) differ in growth with more advanced phenology, thinner leaves and higher photosynthetic rates and (ii) show greater plasticity for these traits across gardens. Genetic differences observed between population ranges for each species would indicate that evolutionary changes could have favoured *A. negundo* and *A. platanoides* invasiveness in France and Canada, respectively. To date, although invasive trees have become a major concern around the world, most studies have used herbaceous species to test for phenotypic trait differences between native and invasive populations. Consequently, little is known about the adaptive evolution processes that might have occurred in invasive tree populations. This study is one of few that directly examine genetic differentiation in invasive tree species using common gardens in both native and introduced ranges.

Material and Methods

Study species

Acer negundo L. (Boxelder or Manitoba maple) is a deciduous mid-successionnal tree species native to North America, with a wide distribution extending from southern Alberta and central Manitoba to north-eastern Texas and New Jersey (Medrzycki 2007). Mainly confined within flood-plains and riparian systems, it can also occur in dry coniferous forests, oak savannas and grasslands (Ward et al. 2002; Dewine and Cooper 2008). Fast growing but generally not exceeding 60 years of age (Maeglin and Ohmann 1973), the species is dioecious and protandrous with both wind dispersed pollen and seeds (Erfmeier et al. 2011). Intentionally introduced in Europe at the end of the 17th century (first known date is 1688 in England) to be later used as an ornamental tree species (Kowarik 2003), *A. negundo* is currently considered as invasive throughout southern, central and eastern Europe where it mostly occurs in riparian habitats characterized by high rate of flood disturbance and high soil nutrient level (Porté et al. 2011; Lamarque et al. 2012). However, it has also widely spread to form monospecific stands under drier conditions faraway from rivers, for instance along roadsides, industrial wastelands or dry ruderal sites (Erfmeier et al. 2011).

Acer platanoides L. (Norway maple) is the most widespread native maple in Europe, with a distribution range occurring from southern Scandinavia to northern Spain and northern Greece southward and to the Ural Mountains eastward and extending until Asia Minor and northern Iran (Santamour and McArdle 1982). The species is shade tolerant and generally found in mixed forests in lowlands, wide river valleys and low mountain areas (Nowak and Rowntree 1990). Introduced in the

United States in 1756 and in Canada in 1778, it has commonly been planted during the latter half of the 20th century as an ornamental shade tree (Nowak and Rowntree 1990; Wangen and Webster 2006). Tolerating a wide range of conditions (Lapointe and Brisson 2011), it has spread into urban woodlands and intact forests of northeastern North America as well as montane forests of the northern Rocky Mountains where it impacts under- and over-storey biodiversity and macro-invertebrate communities (Webb and Kaunzinger 1993; Bertin et al. 2005; Reinhart et al. 2005, 2006). Despite some dispersal limitation (Martin and Canham 2010), *A. platanoides* is currently considered as one of the most common exotic invasive tree species in North America (Fang 2005; Martin al. 2010).

Common garden experiment

Two common gardens were established in Canada (Koffler Scientific Reserve at Joker's Hill, King City, ON; 44.03'N, 79.29'W) and in France (INRA Pierroton research station, Cestas, Gironde; 44°44'N, 0°46'W) (see Table 1 for climate and soil characteristics). Each garden was located both in the native range of one maple tree species and in the introduced range of the other. Seeds were collected during the fall 2006 from ten native (Canada) and ten invasive (France) populations of *Acer negundo* and from ten native (France) and six invasive (Canada) populations of *Acer platanoides* (Appendices 15-17). For each species, populations were haphazardly selected among a pool of 40 populations naturally occurring in France and Ontario, Canada. Seeds were harvested from 10 to 13 maternal trees in each source population with approximately 300 seeds per tree. In February 2007, seeds from each maternal tree were placed into a string net with humid vermiculite, and were submitted to a cold treatment (14 weeks at 5°C in a cold chamber) at the INRA Pierroton research station, France. In spring 2007, seeds were sown into plant tubs with a 2/3:1/3 mix of compost and sand at the French nursery. A total of 25 seeds were sown per maternal tree, *i.e.* 250 seeds per source population. Then in late winter 2008, seedlings were planted in the gardens. Maternal effects were minimized by choosing seedlings with similar height and diameter. Both common gardens had the same surface of 0.5 ha and the same design with 4 blocks of 6 rows. Seedlings were randomly assigned to one of the 4 blocks and represented 6 to 13 maternal trees per population. On average, a total of 40 seedlings were planted per population, leading to 365 individuals per block and 1460 per garden (2 species x 2 continents x 6 to 10 populations x 40 seedlings). In each garden, seedlings were spaced 0.5 m apart with rows separated by 1 m. They were watered on the planting date in both gardens and received ambient rainfall hereafter.

Growth

In both gardens, height and stem collar diameter of each individual were measured every year from 2008 to 2010. Height measurements were carried out using a graduated pole to 0.01 m accuracy while stem collar diameters were measured using an electronic calliper to 0.01 mm accuracy. For all analyses, we used final height and stem diameter (2010) to minimize transplantation effect.

Phenology

Timing of leaf unfolding (LU) was monitored in the two common gardens during two consecutive years (2009 and 2010). Each of the 1460 seedlings was examined every week during a month (from mid-March and late-April in the France and Canada gardens, respectively) for bud development. We recorded the development stage of apical buds from bud dormancy to leaf unfolding using a four stage scale (Vitasse et al. 2009b). For each seedling, leaf unfolding was considered reached when one of the leaves was fully expanded (stage n° 4). Leaf unfolding date (day of the year, DOY) was then estimated by linear regression between two measurement campaigns. For each population, leaf unfolding date was calculated as the average of the estimated dates for each seedling ($n = 25$).

Gas exchange

For both species, gas exchange and leaf morphology were measured in each garden on 6 native and 6 invasive populations with 7 individuals per population, leading to a total of 168 seedlings sampled per garden. Populations were randomly chosen in the France garden and the same were kept for measurements in Canada. Gas-exchange measurements were carried out using a portable steady-state, flow-through chamber (PLC6 (U) broad) connected to an infrared gas analyser (CIRAS-2, PP Systems, Hitchin, UK) equipped with CO_2, temperature, humidity and light control modules. Gas exchange was measured inside a sealed cuvette of 2.5 cm^2 with a CO_2 concentration of 380 ± 3 ppm, a temperature of 22 ± 0.5°C and a relative humidity of 80 ± 10 %. All measurements were made at saturated light (PPFD = 1500 $\mu mol.m^{-2}.s^{-1}$) in order to obtain a light-saturated assimilation rate per unit leaf area (A_{area}, $\mu mol\ CO_2.m^{-2}.s^{-1}$; maximum assimilation rate at ambient CO_2). Prior to each measurement campaign, the gas analyser was calibrated in the laboratory using 400 ppm standard gas, while full CO_2 and H_2O zero and differential calibrations were performed in the field after a set of six measurements. Photosynthesis rates were measured during summer 2009 for *A. negundo* and summer 2010 for *A. platanoides*. Both years, two to three consecutive weeks were required in each garden to complete the photosynthetic measurements due to the need of sunny days. In France and in Canada, measurements were always done between 8.00 and 11.00 solar time on fully expanded sunny leaves. Two to three measurements were carried out on each individual, and data were recorded when assimilation curves remained stable during more than 20 s (CIRAS-2 graphing screen).

Leaf morphology and biochemistry

After gas exchange measurements, three to five fully expanded leaves were collected per individual. Leaf area was determined using a planimeter (Light Box model, Gatehouse, Scientific Instruments LTD, Norfolk, UK). Leaves were then placed in an oven at 65°C until constant dry weight and leaf dry mass was measured with an electronic weigh scale (Explorer Pro, EP 114 model, Ohaus Corporation, Pine Brook, NJ, USA). Leaf mass per area index (LMA, $g.m^{-2}$) was calculated as the ratio of leaf weight by leaf area. Finally, leaf samples were also used to analyze leaf nitrogen content. Leaves were crushed to a powder with a ball mill (MM 200, Fisher Bioblock Scientific, France) and nitrogen content (N_{mass}, %) was analysed using an elementary analyser Eager 300 CHNOS (FlashEA 1112, ThermoElectron Corporation, Waltham, MA, USA). Nitrogen content per leaf area (N_{area}, $g\ N\ m^{-2}$) was calculated as the product of N_{mass} and LMA and the photosynthetic N-use efficiency (PNUE, $\mu mol\ CO_2.g^{-1}N.s^{-1}$) as the ratio of A_{area} by N_{area}.

Statistical analyses

Statistical analyses were conducted separately for each species. Probability of survival was compared between ranges using a generalized linear model with binomial distribution and logit link function (procedure GENMOD in SAS, version 9.1, SAS Institute, Cary, NC, USA). Differences in seedling growth, phenology, leaf physiology and morphology were tested with a generalized linear mixed model (procedure MIXED, REML method in SAS, version 9.1, SAS Institute, Cary, NC, USA). Overall differences in trait were studied by treating location of garden (France or Canada), range (native or introduced) and the location x range interaction as fixed factors and block nested within location, population nested within range and the location x population nested within range interaction as random factors. Random effects were further assessed using a log likelihood ratio test from the full and reduced models. A significant range effect for a given trait indicated overall genetic differentiation between native and invasive populations. Differences in each trait were also analysed for each garden separately, with range as a fixed factor and block and population nested within range as random factors. Phenotypic plasticity was examined here at the population-level as an average across individuals from each population (Richards et al. 2006; Williams et al. 2008), as opposed to the genotype-level. Plasticity was reported when populations of a same range exhibited differences for a trait between the two gardens (*i.e.* a significant location effect). Differences in the magnitude of plasticity were indicated when the interaction location x range was significant. The magnitude of plasticity of each range for a given trait was calculated as follows: $[(\text{trait}_{\text{France}} - \text{trait}_{\text{Canada}})/\ \text{trait}_{\text{France}}]*100$. Lastly, phenological sensitivity was further studied for native and invasive populations of both species. Mean temperature values in 2009 and 2010 were calculated for the same period of time in both the Canadian and French gardens, from 1 January to leaf unfolding dates. Linear regressions were then fitted between temperature and leaf unfolding. Slopes of the corresponding linear regressions were used to obtain the shifts in leaf phenology per degree increase in temperature (day °C^{-1}) and thus to compare phenological sensitivity to temperature between ranges (Vitasse et al. 2009a).

Results

Genetic differentiation

Survival and growth

Survival rate of *A. negundo* significantly differed between ranges ($\chi^2 = 75.23$, $P < 0.0001$; Fig. 1a; see Appendix 18 for mean values). Seedlings from native populations survived better than those from invasive populations both in Canada (96% *vs.* 73%; $\chi^2 = 74.77$, $P < 0.0001$) and in France (74% *vs.* 63%; $\chi^2 = 11.21$, $P = 0.0008$). In contrast, no significant differences in survival were found between ranges for *A. platanoides* ($\chi^2 = 1.14$, $P = 0.2851$; Fig. 1c). Seedlings from native and invasive populations had a survival rate averaging 54% and 71% in Canada and France, respectively.

Diameter significantly differed between ranges of *A. negundo* with seedlings from invasive populations growing larger in France relative to those from native populations (significant range effect; Table 2a, Fig. 1b). We did not observe any difference in diameter between native and invasive genotypes growing in Canada (Fig. 1b). Individuals from invasive populations also grew taller in the French gardens but differences in height were not significant due to high variation for this trait (CV > 58%). For *A. platanoides*, seedlings from native and invasive populations exhibited similar diameters and heights in both gardens (Table 2b, Fig. 1d).

Phenology and ecophysiology

Leaf unfolding significantly differed in the two locations between seedlings of *A. negundo* from native and invasive populations (Table 2a, Fig. 2a). In the Canadian garden, native populations unfolded significantly earlier both in 2009 and 2010. In France, seedlings from invasive populations flushed significantly later in 2009 but earlier in 2010. In contrast, seedlings of *A. platanoides* from native and invasive populations always unfolded at the same time in the two gardens (Table 2b, Fig. 2e).

We found significant genetic differentiation between native and invasive populations of *A. negundo* for all traits related to leaf physiology and morphology (significant range effect; Table 2a, Fig. 2b-d). In particular, native populations expressed greater photosynthetic capacities with significantly higher A_{area} and $\mathrm{N}_{\mathrm{area}}$ as well as greater LMA in both the Canadian and French common gardens. Contrastingly, native and invasive populations of *A. platanoides* showed weak genetic differentiation in physiological and morphological traits. Overall, significant genetically based differences were observed in PNUE and LMA (Table 2b). However, native and invasive populations differed in France only with native populations expressing significant higher LMA, lower PNUE and marginally higher $\mathrm{N}_{\mathrm{area}}$ (Fig. 2f-h).

Phenotypic plasticity

Survival and growth

Survival of *A. negundo* seedlings significantly differed between the two common gardens ($\chi^2 = 64.65$, $P < 0.0001$). After two years, survival was greatest in Canada (85%) than in France (68%). Survival also differed between gardens for seedlings of *A. platanoides* ($\chi^2 = 33.06$, $P < 0.0001$) and was greatest in France (71%) than in Canada (54%).

We found significant differences in diameter and height between gardens for both species (significant location effect; Table 2). Growth conditions were better in France where seedlings grew taller and larger thanks to a longer growing season. Moreover, we detected a significant difference in growth plasticity between ranges for *A. negundo* (significant location x range effect; Table 2): diameter increased by 48% *vs.* 35% between the Canadian and the French garden for seedlings from invasive and native populations, respectively. Seedlings of *A. platanoides* from native and invasive populations did not differ in growth plasticity and for both ranges, diameter and height increased by 40% and 65% between Canada and France, respectively.

Phenology and ecophysiology

Dates of leaf unfolding differed between gardens for both species (Table 2). Mean leaf unfolding occurred 27 and 40 days earlier in France compared to Canada for seedlings of *A. platanoides* and *A. negundo*, respectively. Moreover, we found a significant difference in phenological plasticity between ranges for *A. negundo* (Tables 2 and 3). According to temperature, reaction norms were linear ($r^2 > 0.90$, P

< 0.05) but the magnitude of phenological plasticity was slightly higher for seedlings from invasive populations (3.24 ± 0.12 days degree^{-1}) relative to conspecifics from their native range (2.41 ± 0.45 days degree^{-1}). Seedlings of *A. platanoides* from native and invasive populations did not differ in phenological plasticity, and leaf unfolding advanced by 2.6 ± 0.5 days degree^{-1} (Tables 2 and 3).

Seedlings of both species were highly plastic for all leaf physiology and morphology traits studied (Table 2, Fig. 2b-d and f-h). However, we did not observe any difference in plasticity between ranges for these traits. Seedlings of *A. negundo* from both native and invasive populations had 40% higher A_{area}, 21% higher N_{area}, 19% higher PNUE, 61% higher L_S and 24% lower LMA in the French garden compared to the Canadian garden. Similarly, seedlings of *A. platanoides* increased their A_{area} by 16%, N_{area} by 45%, L_S by 59% and LMA by 15% in France relative to Canada. They showed 37% higher PNUE in the Canada garden.

Discussion

Rapid evolutionary changes in invasive populations of exotic species in response to novel environments have been increasingly documented over the past decade and closely linked to plant invasiveness (Sakai et al. 2001; Parker et al. 2003; Maron et al. 2004b; Buswell et al. 2011). Despite cases of exotic species for which invasive genotypes did not show greater performance than their native conspecifics (Willis et al. 2000; DeWalt et al. 2004; Maron et al. 2004a; Andonian and Hierro 2011), genetic changes have been commonly reported in invasive plants (Blossey and Nötzold 1995; Willis and Blossey 1999; Leger and Rice 2003; Blumenthal and Hufbauer 2007; Feng et al. 2011; Flory et al. 2011a; Eriksen et al. 2012). However, few studies worked on invasive trees (Delmas et al. 2011; Lamarque et al. 2011) and genetic differentiation between native and invasive tree populations was only examined for *Melaleuca quinquenervia* and *Triadica sebifera* to date (Kaufman and Smouse 2001; Siemann and Rogers 2001; Rogers and Siemann 2005; Zou et al. 2007; Franks et al. 2008a, b). Based on reciprocal common gardens, we found genetic differentiation between populations of *A. negundo* from the native and introduced ranges; in particular, invasive populations showed significant faster growth in the introduced range (*i.e.* in France) relative to the native genotypes. In contrast, invasive genotypes of *A. platanoides* did not exhibit greater performance or greater phenotypic plasticity than their native conspecifics.

Genetic differentiation between native and introduced maple populations

Populations of *A. negundo* from the introduced range were genetically different from their native conspecifics with regard to various life-history traits. Concordant with our expectations, they demonstrated faster growth and reduced LMA which may allow them to be well suited to non competitive, nutrient rich and disturbed environments such as the riparian habitats invaded in the non-native range. Our finding is consistent with previous studies that documented genetic-based advantage in growth for invasive over native populations of both exotic grasses (Bastlova and Kvet 2002; Leger and Rice 2003; Blumenthal and Hufbauer 2007; Flory et al. 2011a; Hodgins and Rieseberg 2011) and Chinese tallow tree (*Triadica sebifera*; Siemann and Rogers 2001; Huang et al. 2010). Increased growth may play an important role in the invasion success of the species because growth has been recognized as a major component of plant invasiveness (Grotkopp et al. 2002; van Kleunen et al. 2010;

Lamarque et al. 2011). In particular, it was recently found that French populations of *A. negundo* outcompete co-occurring native tree species through higher growth rate under non-limiting conditions (Saccone et al. 2010; Porté et al. 2011). The absence of difference in growth in the Canadian garden might be due to harsher winter conditions or greater amount of herbivory damage on invasive populations which may have counterbalanced their competitive advantage (Lamarque, personal observations). Insect herbivory significantly affects plant success by reducing growth rate (Marquis 1992) and previous research documented the evolution of the trade-off between increased growth and decreased investment in defense in invasive genotypes of exotic plants (Siemann and Rogers 2003a, b; Maron et al. 2004a; Huang et al. 2010). Thus, invasive genotypes of *A. negundo* might have evolved greater competitive ability at the expense of defense capacities.

Contrary to our prediction, the faster growth and invasive success of *A. negundo* populations from the introduced range is not achieved through increasing net assimilation rate. Indeed, invasive populations showed lower photosynthetic capacity and lower leaf nitrogen contents in the two gardens compared to native conspecifics. This result contrasts with the current literature as studies have documented either no difference between native and introduced populations (Bastlova and Kvet 2002; DeWalt et al. 2004) or physiological advantages of invasive genotypes (Zou et al. 2007; Feng et al. 2011). Invasive populations of *A. negundo* exhibited lower LMA, a characteristic often positively associated with fast-growing plants (Pattison et al. 1998; Nagel and Griffin 2004). Provided the same leaf biomass than native genotypes, invasive ones would thus exhibit greater photosynthetic surface area which would allow greater light use efficiency and carbon assimilation. Invasive populations of *A. negundo* also showed poorer physiological performances but larger investment in the development of aerial structures when compared to native species from invaded communities of southern France (Porté et al. 2011). In consequence, it might be possible that a change in adaptive strategy has occurred in the introduced range favouring genotypes with higher resource allocation to foliage favouring faster growth. This should be disentangled in several years by comparing biomass production between ranges.

Lastly, populations of *A. negundo* from the introduced range significantly exhibited lower survival rates in the two gardens compared to the native genotypes. This suggests a possible trade-off between competitive ability and survival; invasive populations might have evolved towards faster growth at the expense of survivorship. To date, such difference in survival-growth trade-off between native and invasive genotypes has been documented for the annual herb *Ambrosia artemisiifolia* (Hodgins and Rieseberg 2011) and evergreen shrub *Rhododendron ponticum* (Erfmeier and Bruelheide 2010).

In contrast to *A. negundo*, we did not observe differences suggesting any genetically-based differences in phenotype between populations of *A. platanoides* from the native and introduced ranges. First, time since invasion affects the potential for genetic change in invasive species (Williamson 1996), and therefore it might not have been sufficient to enable evolutionary changes to be established (Willis et al. 2000; Franks et al. 2008b). Nonetheless, this seems unlikely given that *A. platanoides* has been present and naturalized in North America for roughly the same period of time as *A. negundo* in Europe (250-300 years; Nowak and Rowntree 1990; Kowarik 2003). Second, maternal effects may have contributed to the lack of difference (Franks et al. 2008a); however, we did not observe any difference in germination. Third, selection for faster growth may have been limited. This might be due to the mid- to late-successionnal life history strategy exhibited by *A. platanoides* with an efficient shade tolerance enabling it to invade closed-canopy forests (Martin and Canham 2010). Finally, selection may have not been intense because populations of *A. platanoides* sampled in Southern Ontario may not contain enough genetic variation in the traits related to growth. This is a concern because molecular analyses comparing genetic diversity between the native and introduced ranges of this species have yet to be done. However, *A. platanoides* has been widely used in landscaping (Nowak and Rowntree 1990; Conklin and Sellmer 2009) and therefore we could expect that multiple introduction events may have occurred and counterbalanced population bottlenecks maintaining genetic diversity in the introduced range.

Increased phenotypic plasticity

Across the two gardens, populations of both *A. negundo* and *A. platanoides* exhibited high levels of plasticity in all studied traits. Consistent with the common consideration that phenotypic plasticity is important for plant invasiveness (Richards et al. 2006), our results also support previous work that experimentally provided evidence for high magnitude of plasticity in invasive populations of exotic plants in general (Poulin et al. 2007; Funk 2008) and exotic maples in particular (Kloeppel and Abrams 1995; Reinhart et al. 2006; Porté et al. 2011). Moreover, the comparison of trait plasticity between native and invasive maple genotypes produced mixed results. We observed a significant genotype-environment interaction for *A. negundo* but not for *A. platanoides*. Similarly, no general pattern has emerged in the literature so far. While a growing number of studies reported greater plasticity of various traits in invasive over native populations of exotic species (Leger and Rice 2003; Chun et al. 2007; Lavergne and Molofsky 2007), others did not find any difference in plasticity between home and away genotypes (Williams et al. 2008; Flory et al. 2011b). Contrasted results were also obtained for the invasive tree *Melaleuca quinquenervia*, with invasive populations showing higher plasticity to water and pH variation than native conspecifics (Kaufman and Smouse 2001) while no divergence in plasticity was found between ranges in response to herbivory (Franks et al. 2008b). Such differences in results between studies are likely due to differences in the genetic diversity available in the introduced range and in adaptive post-invasion evolution (Bossdorf et al. 2005) as well as to variations in the environmental gradients and traits examined.

Invasive populations of *A. negundo* expressed increased phenotypic plasticity in diameter growth and leaf phenology relative to populations in their native range. This significant genotype–environment interaction for growth and phenology suggests the presence of adaptive genetic variation, indicating potential to adapt to warmer conditions. Greater plasticity in growth may enable invasive populations of *A. negundo* to invade various environments by capitalizing more efficiently on favourable conditions (Richards et al. 2006). Increased plasticity in fitness traits for invasive genotypes in response to variation of abiotic conditions has been observed by several studies (Kaufman and Smouse 2001; Chun et al. 2007; Qing et al. 2011). In particular, Zou et al. (2009) found that invasive populations of *Triadica sebifera* had greater performance than native ones under benign conditions. Interestingly, the fact that invasive populations of *A. negundo* from France grew significantly better in the French garden and flushed significantly later in Canada relative to their native conspecifics suggests that they might have evolved to be locally adapted to their new environment (Parker et al. 2003). However, a more complete assessment of such home-site preference will require the use of reciprocal transplant experiments comparing introduced populations from a wider distribution range (Ebeling et al. 2011). Finally, differences in leaf phenology observed between native and invasive populations in response to temperature are in accordance with studies that emphasized genetic differentiation in flowering phenology for invasive herbaceous species (Bastlova and Kvet 2002; Eriksen et al. 2012). Based on two common gardens, Williams et al. (2008) also highlighted the importance of climatic conditions and growing season length in controlling flowering of native and invasive populations of *Cynoglossum officinale* but did not observe difference in plasticity between ranges. Overall, the greater sensitivity of invasive populations of *A. negundo* to temperature might help them to keep colonizing new areas in Europe as invasive species with flexible phenologies are expected to benefit from increased system variability and longer growing seasons (Wolkovich and Cleland 2011).

Conclusion

Using a quantitative genetic approach, we provide new insights into tree invasions showing that invasive *A. negundo* populations may have evolved faster growth and greater phenotypic plasticity in response to new environments in France. In contrast, the success of *A. platanoides* in Canada may be based on other mechanisms than evolutionary changes in the focal traits. Further investigations would be required to evaluate the importance of genetic differentiation *vs.* phenotypic plasticity (Monty and Mahy 2010), assess whether plasticity is adaptive (Richards et al. 2006) and test local adaptation with populations from a wider distribution range. More importantly, several mechanisms can explain genetic differences between native and invasive populations, in particular demographic bottlenecks, multiple introductions, hybridization and natural selective forces following novel biotic and abiotic pressures (Sakai et al. 2001; Bossdorf et al. 2005; Dlugosch and Parker 2008). Consequently, neutral genetic marker based analyses are needed to determine the role of founder effects and post-introduction selection in shaping exotic maple invasions. Such information would also have implication in conservation issues as invasive species showing decreased genetic variation at resistance loci might be more prone to control (Müller-Schärer et al. 2004). Alternatively, evidence for adaptive selection would suggest that invasive trees would represent suitable models for understanding adaptation of tree species in general to climate change.

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Table 1. Climate and soil characteristics in common gardens established in Canada (King City, Ontario) and France (Cestas, Gironde).

	Canada	France
Mean annual rainfall (mm)	853.8	830.5
Mean annual temperature (°C)	8.1	12.7
Mean January high temperature (°C)	-1.8	10.5
Mean January low temperature (°C)	- 10.3	2.0
Mean July high temperature (°C)	27.2	26.7
Mean July low temperature (°C)	15.5	13.2
Type of soil	clay	sandy
Soil nitrogen (%)	0.18 ± 0.03	0.08 ± 0.01
Soil carbon (%)	3.02 ± 0.49	2.13 ± 0.16
Soil carbon/ nitrogen ratio	16.95 ± 0.68	25.57 ± 2.88
Soil pH	7.46 ± 0.09	4.22 ± 0.21

Note: King City climate data from the Canada's National Climate Archive (climate normals 1996-2011 from Toronto Buttonville Airport station, ON); Cestas climate data from the French National Weather Service (climate averages 1996-2011 from the INRA research station, Gironde).

Table 2. Generalized linear mixed models (GLMM) analyses of traits related to growth (diameter and height), phenology (LU), physiology (A_{area}, $\mathrm{N}_{\mathrm{area}}$, PNUE) and leaf morphology (LMA) for native and invasive populations of A) *Acer negundo* and B) *Acer platanoides* grown in two reciprocal common gardens. See Appendix 18 for mean values of traits.

		Diameter	Height	LU 2009	LU 2010		A_{area}	$\mathrm{N}_{\mathrm{area}}$	PNUE	LMA
Source of variation	*df*	*F* or LLR	*F* or LLR	*F* or LLR	*F* or LLR	*df*	*F* or LLR	*F* or LLR	*F* or LLR	*F* or LLR
A) *Acer negundo*										
Fixed effects										
Location	1	328.76***	16.32***	12148.90***	4376.48***	1	110.49***	41.42***	11.24**	76.61***
Range	1	16.91***	0.01	174.13***	32.00***	1	18.95**	96.19***	3.90†	51.55***
Location x range	1	24.26***	1.07	55.15***	427.75***	1	1.18	0.50	0.72	1.35
Random effects										
Population (range)	18	5.90*	1.50	1.10	1.50	10	0	0	0	0.50
Location x population (range)	18	1.90	0.90	1.50	0	10	0	0	0	0
B) *Acer platanoides*										
Fixed effects										
Location	1	89.88***	31.97***	5586.78***	1505.49***	1	8.05*	269.80***	61.30***	70.97***
Range	1	0.03	0.34	0.07	0.01	1	4.01†	3.00	9.42**	7.27*
Location x range	1	0.01	0.23	0.22	0.19	1	0.08	3.18	0.55	0.81
Random effects										
Population (range)	14	4.20	0.30	4.70	28.00	10	0	0.50	0	1.70
Location x population (range)	14	3.50†	0	0	0.40	10	0	0.10	0	0

Notes: *F* values are given for fixed effects while log likelihood ratios (LLR) are given for random effects. Survival data were calculated at the population level; thus, there is no χ^2 value for population (range) and location x population (range). See text for definition of terms. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Slope of the regression (day degree^{-1}) between the date of leaf unfolding and temperature[a] in 2009 and 2010 for native and invasive populations of *Acer negundo* and *Acer platanoides* monitored in two gardens (Canada *vs*. France).

	Leaf unfolding/ T° (day degree^{-1})		
	Slope	SE[b]	r^2
Acer negundo			
Native populations	- 2.41*	0.45	0.93
Invasive populations	- 3.25**	0.12	0.99
Acer platanoides			
Native populations	- 2.64*	0.58	0.91
Invasive populations	- 2.61*	0.55	0.92

Notes: [a] Mean temperature from 1 January to 25 March for *Acer negundo* and from 1 January to 30 March for *Acer platanoides*, [b] SE of the linear regression slope. * $P < 0.05$, ** $P < 0.01$.

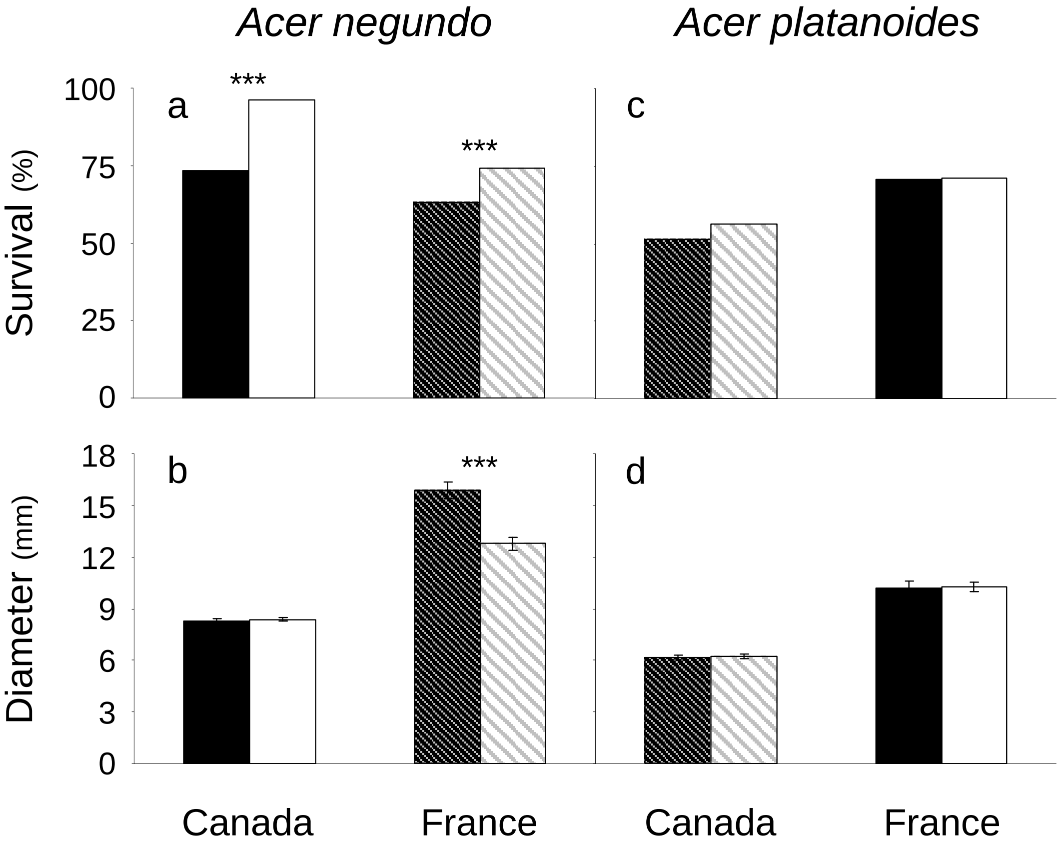

Fig. 1. Differences in survival and diameter between native (white bars) and invasive (black bars) populations of *Acer negundo* (a, b) and *Acer platanoides* (c, d) grown in two common gardens (Canada *vs*. France). The invasive range of each species is represented with hatchings. Values represent means ± SE for both native and invasive populations. *** *P* < 0.001.

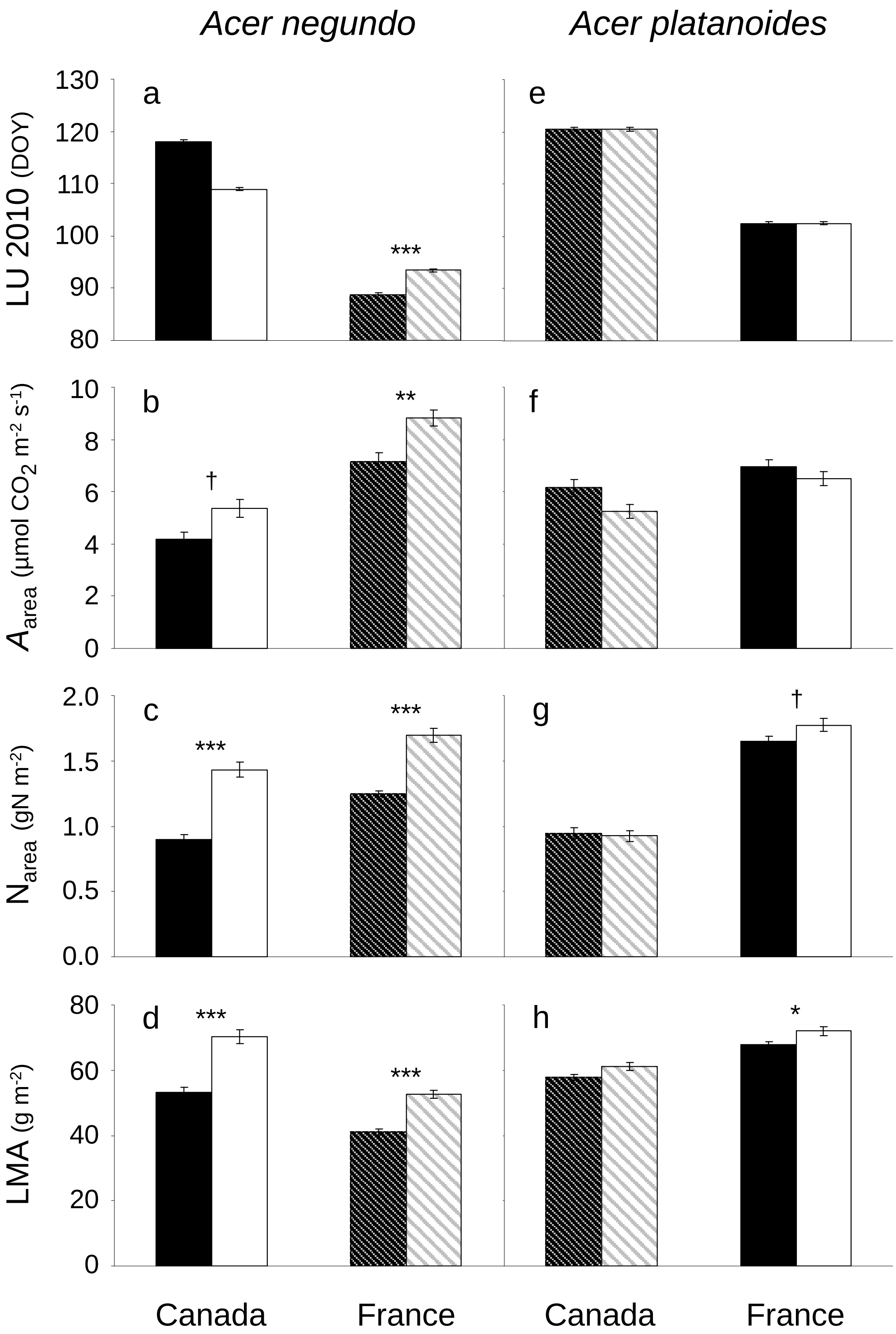

Fig. 2. Differences in phenology (LU), physiology (A_{area} and N_{area}) and leaf morphology (LMA) between native (white bars) and invasive (black bars) populations of *Acer negundo* (a-d) and *Acer. platanoides* (e-h) grown in two common gardens (Canada *vs*. France). The invasive range of each species is represented with hatchings. Values represent means ± SE for both native and invasive populations. See text for definition of terms. † $P < 0.06$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Chapter 5

A comparison of the plastic response to nutrients between native and invasive populations of an invasive tree species

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Abstract

Phenotypic plasticity is a key mechanism associated with the spread of exotic plants and previous studies have found that invasive species are generally more plastic than co-occurring species. Comparatively, the evolution of phenotypic plasticity in plant invasion has received less attention, and in particular, the genetic basis of plasticity is largely unexamined. Native from North America, *Acer negundo* L. is aggressively impacting the riparian forests of southern and eastern Europe thanks to higher plasticity relative to co-occurring native species. We therefore tested here whether invasive populations have evolved increased plasticity since introduction. The performance of 1152 seedlings from 8 native and 8 invasive populations was compared in response to nutrient availability. Irrespective of nutrients, invasive populations had higher growth and greater allocation to above-ground biomass relative to their native conspecifics. More importantly, invasive genotypes did not show increased plasticity in any of the 20 traits examined. This result suggests that the high magnitude of plasticity to nutrient variation of invasive seedlings might be pre-adapted in the native range. Invasiveness of *A. negundo* could be explained by higher mean values of traits due to genetic differentiation rather than by evolution of increased plasticity.

Key words

Invasion, *Acer negundo*, phenotypic plasticity, nutrient, pre-adaptation, trait

Introduction

Phenotypic plasticity has been widely recognized as an important feature for plants to cope with environmental changes [1,2]. Numerous studies have shown that plants are plastic for a large array of traits related to structure, development, metabolic activity, morphology, physiology, phenology, and reproduction [3-10]. Phenotypic plasticity has also been classified as a major determinant of the success of invasive species by increasing fitness relative to native species in recipient communities [11,12,13]. Broader distributions of alien species are correlated with higher levels of plasticity in response to increasing resource availability [14], and on artificial gradients, invasive species are also more plastic than co-occurring native or non-invasive species [15-20]. Davidson et al. [21] recently synthesized this work via a meta-analysis of 75 pairs of invasive/native species concluding that invasive species do express greater phenotypic plasticity than native species irrespective of the response traits measured. However, there are instances that did not support this pattern [22-25], and it has been suggested that the success and fitness advantage of invasive species can be mediated by the expression of constant higher mean trait values across different environments and not necessarily by the plasticity of these traits [26-29]. For instance, invasive species frequently possess higher trait values for growth rate [30,31,32], lower leaf mass per area [30,33, see 34 for review], and advanced leaf unfolding and flowering periods [35,36, see 37 for review]. Phenotypic plasticity should therefore be considered in combination with mean trait values when testing for plant invasiveness.

Higher plasticity levels of invasive species are generally hypothesized to be related to post-introduction evolution of phenotypic plasticity [13,38,39]. In this regard, intraspecific contrasts across environmental gradients have been analyzed in the following cases: (i) between populations from native and invasive ranges [40,41] and (ii) between populations within the invasive range [12,42,43]. Overall, no general pattern has emerged to date. Invasive populations of *Senecio inaequidens* were for instance more plastic than their native conspecifics in response to fertilization [44] while no difference was observed between native and invasive populations of *Microstegium vimineum* across a large array of environments [45]. Variation in light and soil moisture availability induced differences in plasticity for above-ground biomass and leaf mass per area among invasive populations of *Microstegium vimineum* but not for reproduction-related traits among invasive populations of *Polygonum cespitosum* expressed similar plasticity for [42,43]. Pre-adapted plasticity might therefore be a common feature of several invasive plants, and it should now be more explicitly tested.

A total of 357 tree species has been reported to be invasive worldwide disrupting major native ecosystem structure and functioning [46,47,48]. Invasive trees are thus appropriate models to evaluate the role of ecological and evolutionary processes in invasion given their large impacts, frequency, and longevity [49-53]. To date, most studies examining the importance of phenotypic plasticity in tree invasion compared invasive *vs.* native tree species [15,39,54,55]. With the exception of *Melaleuca quinquenervia* and *Triadica sebifera* [39,56], the genetic differences in plasticity between native and invasive populations of exotic trees are unexamined.

Porté et al. [57] recently found that the invasive tree *Acer negundo* significantly expressed higher magnitude of phenotypic plasticity than its co-occurring native species with increasing environmental resources, and particularly nutrient availability. The purpose of this study was therefore to examine the genetic basis of plasticity in *A. negundo*, *i.e.* to determine whether higher plasticity of invasive populations is due to post-introduction evolution or pre-adaptation in the native range. The performance of native and invasive populations of *A. negundo* was compared across a gradient of nutrient availability. Life-history traits related to growth, physiology, leaf morphology and biomass and known to promote plant invasiveness [31,32] were measured. We hypothesize that invasive populations possess greater plasticity in growth and associated traits relative to populations from the native range. These findings would support the idea that plasticity could have evolved in the introduced range. In contrast, the absence of difference in plasticity between populations from native and invasive ranges would indicate that higher plasticity of invasive populations of *A. negundo* could be due to pre-adaptation in the native range.

Material and Methods

Studied species

Acer negundo L. (Box Elder or Manitoba maple) is a widely distributed mid-successional species native to North America. Its distribution range extends from southern Alberta and central Manitoba to Mexico and Guatemala southward and from central Montana to New England states and central Florida eastward [58,59 but see 60]. This species is frequently found in floodplains and riparian habitats but can also occur in dry coniferous forests, oak savannas, and grasslands [61,62]. . *A. negundo* was intentionally introduced in the Old Continent at the end of the seventeenth century, *i.e.* in 1688 in England, and in France in 1749 [60,63].

Currently, *A. negundo* is highly invasive throughout southern, central and eastern Europe [60,64, DAISIE database http://www.europe-aliens.org). It frequently occurs not only in riparian habitats characterized by high rate of flood disturbance and high soil nutrient level [65,66] but also under drier conditions along roadsides, industrial wastelands, and dry ruderal sites [52,67].

Experimental design

Seeds of *A. negundo* were harvested between September and November 2009 from eight native populations sampled in Ontario and Quebec, Canada and from eight invasive populations located in the Landes and Gironde departments of Aquitaine region, Southern France (Table 1, Appendix 19). No specific permissions were required for these locations that are not part of protected areas and do not involve endangered species. All native and invasive populations were sampled from riparian forests. Populations in the invasive range were distributed within the Adour-Garonne river basin. Seeds came from 9 to 12 maternal trees in each source populations with maternal trees randomly selected and at least 10 m apart. In February 2010, 30 seeds per maternal tree were subjected to a cold treatment (14 weeks at 5°C in a cold chamber) at the INRA research station of Pierroton, France (44°44'N, 0°46'W). In spring 2010, 27 seeds per maternal tree were sown into 4 L (15 x 15 x 17.7 cm) pots filled with a commercial sphagnum peat soil mixture (organic matter 80%, pH = 6). We first sowed three seeds per pot until germination and then kept one seedling in each pot thereby generating a total of 90 seedlings per source population. Pots were then placed under a greenhouse that was side-opened to permit wind and insects to enter. We did not control light and temperature that approximated ambient conditions. Seedlings were watered twice a week to saturation.

A split-plot design was used with nutrient level as the fixed main effect and range of *A. negundo* populations (native or invasive) as the fixed sub-effect with all native and invasive populations subjected to three nutrient levels. We selected 72 seedlings from 8 to 10 families (*i.e.* maternal trees) per population for a total of 1152 seedlings structured as follows: 6 blocks x 3 nutrient levels x 2 ranges x 8 populations x 4 individuals. The experiment was initiated on February 17th, 2011 and lasted 147 days. Nutrients were applied on the 25th, 53th, 81st and 109th days of the experiment. The nutrient treatment corresponded to the addition of the complete slow release 16-7-15 (NPK plus micronutrients) fertiliser Floranid Permanent (Compo France SAS, Levallois-Perret, France). In the low nutrient level (N0), seedlings did not receive any additional fertilizer. In the medium and high nutrient levels (N1 and N2, respectively), seedlings received four fertilizer doses equivalent to 0.125 g and 0.500 g N each, for a total of 0.500 g and 2 g N, respectively. The high nutrient level corresponded to the nutrient availability encountered by *A. negundo* populations in soils of the invaded riparian habitats of southern France [68,69]. A previous study conducted *in situ* also showed that invasive individuals of *A. negundo* had a leaf N content averaging 1.17 $gN.m^{-2}$ [57]. The N0 and N1 treatments thus represent levels of nutrient that are below the average field conditions in the introduced range.

Gas exchange

Photosynthetic rate measurements were performed on 192 seedlings. In each treatment, four individuals from different families and blocks were randomly sampled per source population. The measurements were done on sunny days between June 20th and July 7th. Leaf gas exchange measurements were carried out with a portable steady-state flow-through chamber (PLC6) connected to an infrared gas analyser (CIRAS-2, PP Systems, Hitchin, UK) equipped with temperature, humidity, light and CO_2 control modules. Net gas exchanges were measured within a sealed cuvette of 2.5 cm^2, with an air CO_2 concentration of 380 ± 3 ppm, a temperature of 22 ± 0.5°C and a relative humidity of 80 ± 10 % of ambient, controlled by regulating the flow diverted through a desiccant. To obtain the maximum assimilation rate per unit leaf area (A_{area}, µmol $CO_2.m^{-2}.s^{-1}$) at ambient CO_2, leaves were illuminated with a red-blue light source attached to the gas exchange system and maintained at saturated light (PPFD = 1500 µmol $PAR.m^{-2}.s^{-1}$). Prior to the measurements, the gas analyser was calibrated in the laboratory using 400 ppm standard gas, while full CO_2 and H_2O zero and differential calibrations were performed in the field after each set of six measurements. Up to three measurements were carried out on each sampled individual, and data were recorded when assimilation curves remained stable for more than 20 s. All measurements were taken between 8.00 and 11.00 solar time on fully expanded and sun-exposed leaves to avoid midday stomatal closure.

Leaf morphology and biochemistry

Leaf nitrogen content and morphological traits were measured on 288 seedlings representing six individuals per population and per treatment (including those used for gas exchange measurements). Leaves were sampled on the same days as the photosynthetic rate measurements. Three to five leaves were collected per sampled individual. Leaf surface area was measured with a planimeter (Light Box model, Gatehouse, Scientific Instruments LTD, Norfolk, UK) and we average leaf size (L_s, cm^2) was calculated. Leaves were then placed in an oven at 65°C until constant dry weight and leaf dry mass was later weighed with an electronic weighing scale (Explorer Pro, EP 114 model, Ohaus Corporation, Pine Brook, NJ, USA). Leaf mass per area index (LMA, g leaf.m^{-2} leaf) was calculated as the ratio of leaf weight by leaf area. Finally, leaf samples were crushed to a powder with a ball mill (MM 200, Fisher Bioblock Scientific, France) and leaf nitrogen content (N_{mass}, %) was determined using an elementary analyser Eager 300 CHNOS (FlashEA 1112, ThermoElectron Corporation, Waltham, MA, USA). The maximum assimilation rate per unit leaf mass (A_{mass}, µmol $CO_2.g^{-1}.s^{-1}$) was calculated as the A_{area} to LMA ratio, the leaf nitrogen content per leaf area (N_{area}, g $N.m^{-2}$) as the product of N_{mass} and LMA, and the photosynthetic N-use efficiency (PNUE, µmol $CO_2.g^{-1}$ $N.s^{-1}$) as the A_{area} to N_{area} ratio.

Growth and biomass

A total of seven individuals died during the course of the experiment and therefore, final height and stem collar diameter of 1145 seedlings were recorded on July 4th. A graduated pole to 0.01 m accuracy was used to record heights, and diameters were measured with an electronic calliper to 0.01 mm accuracy. The 288 individuals previously used for morphological measurements were harvested on July 14th after 147 days of growth. Above-ground biomass was separated into stems and leaves, and roots were separated from soil and washed. Biomass was oven-dried at 65°C until constant dry weight and further weighed using an electronic weighing scale (Explorer Pro, EP 114 model, Ohaus Corporation, Pine Brook, NJ, USA). The following traits were calculated: total biomass (W_t, g), above-ground biomass (W_a, g), leaf biomass (W_l, g), stem biomass (W_s, g), root biomass (W_r, g), total leaf area (A_l, m^2), leaf weight ratio (LWR, g leaf.g^{-1} plant), stem weight ratio (SWR, g stem.g^{-1} plant), root weight ratio (RWR, g root.g^{-1} plant), root:shoot ratio (RSR, g.g^{-1}) and leaf area ratio (LAR, m^2 leaf.g^{-1} leaf).

Statistical analyses

Differences in traits were tested with a generalized linear mixed model that was fit to a split-plot design (procedure MIXED, REML method in SAS, version 9.2, SAS Institute, Cary, NC, USA) [70]. We used nutrient level, range, and the interaction of nutrient level x range as fixed factors whilst block, block x range, population nested within range, and the interaction of nutrient level x population nested within range were treated as random factors. To account for the influence of plant size on biomass allocation [71 and references herein], we used total biomass as a covariate when we tested the following traits: RSR, LWR, SWR, RWR, A_l and LAR. Type III sums of squares were used for the calculation of F statistics. Random effects were further evaluated using a log likelihood ratio (LLR) test from the full and reduced models. All factors were identified significant at alpha < 0.05. A significant range effect for a given trait indicated an overall genetic differentiation between seedlings from native and invasive populations. Moreover, phenotypic plasticity was examined here at the population-level [13,72]. A significant effect of nutrient level indicated plasticity for a given trait. The difference in plasticity of a given trait between seedlings from native and invasive populations was reported when the interaction of nutrient level x range was significant. The variation of trait of native and invasive seedlings was also reported as follows: $[1-(\text{trait}_{env2/}\text{trait}_{env1})]*100$. Lastly, we calculated the Relative Distance Plasticity Index (RDPI) [73], and the Plasticity Index (PI) [5] for two experimental nutrient level changes: low-to-medium and medium-to-high as follows:

$$\text{RDPI} = \frac{|\text{mean(env1)} - \text{mean(env2)}|}{|\text{mean(env1)} + \text{mean(env2)}|}$$

$$\text{PI} = \frac{[\text{mean(env1)} - \text{mean(env2)}]}{[\max(\text{mean(env1)}, \text{mean(env2)})]}$$

For each trait, the two indexes were calculated for each population using mean values in each treatment (*i.e.* nutrient level). The difference in RDPI and PI between native and invasive ranges was examined using a generalized linear mixed model with range as a fixed factor and population nested within range as a random factor.

Results

Overall trends

Irrespective of nutrients, individuals of *A. negundo* from invasive populations expressed significantly greater heights and smaller diameters than their native conspecifics (significant range effect; Table 2; Fig. 1A, B; see Appendix 20 for means per treatment). There was no significant difference in maximum assimilation rates (A_{area} and A_{mass}; Fig. 1C), and invasive seedlings had lower leaf nitrogen contents (N_{area} and N_{mass}; Fig. 1D) and greater PNUE (Table 2). Invasive seedlings also had lower average leaf size and LMA (Table 2; Fig. 1E). There were no statistical differences in total and aboveground biomass (Table 2; Fig. 1F). Seedlings from invasive populations however allocated more resources to foliage than to roots, displaying greater A_l, LWR, SWR and LAR, and lower W_r, RSR and RWR compared to seedlings from native populations (Table 2; Fig. 1G, H). Significant genetic variations were found in height among invasive populations (within invasive range: LLR = 5.6, $P = 0.018$; within native range: LLR = 0.6, $P = 0.44$) and in diameter among native populations (within native range: LLR = 14.1, $P = 0.0002$; within invasive range: LLR = 0.5, $P = 0.44$).

Trait plasticity

Seedlings of *A. negundo* responded significantly to increases in nutrients (significant nutrient effect for all traits but LMA and SWR; Table 2; Fig. 2) with increased growth, maximum assimilation rate, total biomass, and above-ground allocation (AGB, TLA, LWR, LAR) and decreased below-ground allocation (RSR, RWR). The change from low-to-medium nutrient conditions had a stronger effect on seedling trait values than the change from medium-to-high nutrient conditions. Individuals of *A. negundo* respectively showed a 19%, 44% and 35% increase in height, maximum assimilation rate and total biomass from low-to-medium nutrient conditions but a 2%, 18% and 9% increase from medium-to-high nutrient conditions (Fig. 2; see Tables 3 and 4 for trait RDPI and PI values). Across all populations, traits such as SWR and LMA showed low plasticity along the nutrient availability gradient (mean $\mathrm{RDPI}_{\mathrm{SWR}} = 0.03$, mean $\mathrm{RDPI}_{\mathrm{LMA}} = 0.07$) while W_l, A_{area} and $\mathrm{N}_{\mathrm{area}}$ exhibited larger changes (mean $\mathrm{RDPI}_{Wl} = 0.21$, mean $\mathrm{RDPI}_{A\mathrm{area}} = 0.22$, mean $\mathrm{RDPI}_{\mathrm{Narea}} = 0.25$).

There were no significant differences in plasticity between seedlings from native and invasive populations for any traits (non-significant nutrient x range effect;

Table 2; Fig. 2). There was also no difference in RDPI or PI for any traits but the $RDPI_{LMA}$ between medium and high nutrient levels did differ (Tables 3 and 4; across the whole gradient, mean trait RDPI = 0.15 and 0.14 and mean trait PI = -0.14 and -0.15 for native and invasive populations, respectively). The magnitude of plasticity differed at the population level for height, maximum assimilation rate, and SWR (significant nutrient x population effect; Table 2).

Discussion

Higher magnitudes of plasticity relative to native species are common in invasive plants, particularly in invasive trees [15,21,74]. Nevertheless, these differences are not necessarily a product of post-introduction evolution and can also be explained by innate characteristics. This null hypothesis was tested and supported in this study using the highly invasive tree species *Acer negundo*. Although increased nutrient availability is a key component of tree recruitment dynamics [75,76], this artificial gradient tested here did not elicit differences in plasticity between native and invasive seedlings. Pre-adapted plasticity to nutrient availability is thus a reasonable explanation for the successful spread of this species, at least at this early stage of development.

The evolution of plasticity in invasive species is relatively infrequent and no consensus has been reached in the literature so far (Appendix 21). Variation in resource conditions lead to differences in plasticity between seedlings from native and invasive populations for perennials *Centaurea stoebe* and *Taraxacum officinale* and trees *Melaleuca quinquenervia* and *Triadica sebifera* [39,56,77,78] but not for the annual grass *Microstegium vimineum*, the biennnial forb *Alliaria petiolata* and the perennial shrub *Clidemia hirta* [40,45,79]. However, a rigorous assessment of the origin and importance of plasticity in plant invasion requires both inter- and intraspecific contrats [39]. In response to nutrient availability, invasive seedlings of *A. negundo*, which had shown increased plasticity relative to than their co-occurring native species across the same resource gradient [57], expressed here similar response for all life-history traits compared to their native conspecifics. Our results therefore reflect innate characteristics of plasticity that would be pre-adapted in the native range. This supports the outcome observed for *Triadica sebifera* in response to water availability: invasive seedlings exhibited greater growth than seedlings of native *Schizachyrium scoparium* but not than their native conspecifics [39]. The only other study that conducted both inter- and intraspecific comparisons across the same resource gradient did not find any difference in plasticity to CO_2 enrichment between native and invasive populations of *Eupatorium adenopherum* and the native congener *Eupatorium japonicum* [80].

Seedlings from native and invasive populations of *A. negundo* significantly differed in most of their traits across the gradient of nutrient availability. Invasive seedlings consistently exhibited higher values for traits associated with invasiveness, *i.e.* higher growth rate, lower LMA, and greater allocation to foliage [30,34]. This supports many other studies which posit that genetically-based advantages in plant size and above-ground biomass for invasive over native genotypes may promote the success of invasive species [81-84]. For instance, invasive individuals of *Melaleuca quinquenervia* and *Triadica sebifera* also outperformed native congeners [39,56,85]. Interestingly, invasive seedlings of *A. negundo* did not achieve greater height growth via physiological advantages but only via a preferential allocation to foliage.

Significant lower leaf nitrogen content and similar maximum assimilation rate were found here. This contradicts recent studies on the genetically-based difference of functional traits in invasive plant species that showed higher values of physiological traits for invasive genotypes [86,87,88]. These divergences might be due to the rapid adaptation of *A. negundo* in its introduced range reflecting a change in adaptive strategy. Whilst plasticity may not have evolved *de novo*, it is possible that most of the traits conferring faster growth (such as greater allocation to above-ground biomass) may have done so to provide a competitive advantage over native species of recipient communities.

Multi-species comparisons in the native range of exotic plant species showed that invasive aliens differed in traits but not in plasticity from their non-invasive alien congeners [26,28], and pre-adaptation of plasticity in invasive plant species might finally be more common than expected. Phenotypic plasticity is a common denominator for invasive plant species but tolerance of invasive genotypes across a broad range of conditions might rely more on a combination of life-history traits rather than on evolved plasticity in the introduced range. This would be the case for *A. negundo* since the species occupies wide and similar ranges of habitats such as wet-rich and dry-poor nutrient riparian forests both in North America and in Europe [52,61,89]. Furthermore, various mechanisms such as founder effects, multiple introductions, and selective pressures can drive genetic differentiation between native and invasive populations. Molecular analyses using neutral markers over large areas sampled including whole native and invasive ranges would thus be necessary to fully understand the role of these factors [90]. Given that there was no consistent variation in traits amongst populations from the invasive range, genetic data would provide valuable information on the origin of those populations sampled in French riparian areas, *e.g.* whether they have all undergone similar selective pressures or come from the same pool of native populations which were not sampled in this study (*i.e.* founder effects).

Conclusions

The origin of increased plasticity in invasive plant species is an important and relatively understudied set of hypotheses. Given the geographical scope of the populations we were able to sample herein, pre-adaptation is a more viable explanation for the high magnitude of plasticity of invasive *A. negundo* seedlings to variation in nutrient availability. Future studies should however test in the native range the response of native and invasive genotypes sampled at broader scales to a combination of abiotic factors in order to test more effectively both the importance of evolved *versus* pre-adapted plasticity and increases in competitive ability of invasive species.

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Table 1. The 16 source populations sampled to examine phenotypic plasticity of invasive tree species *Acer negundo*.

Province/ Department	Collection site	River	Latitude	Longitude	Distance to the nearest population (km)
Native range					
Ontario	Paris	Grand	43°12’27’’N	80°21’58’’W	65
Ontario	Fergus	Grand	43°41’53’’N	80°22’50’’W	65
Ontario	Nicolston	Nottawasaga	44°10’40’’N	79°49’02’’W	18
Ontario	Angus	Nottawasaga	44°18’59’’N	79°53’08’’W	18
Ontario	Toronto Home Smith park	Humber	43°39’06’’N	79°29’44’’W	26
Ontario	Toronto Serena Gundy park	Don	43°43’05’’N	79°21’15’’W	26
Quebec	Sherbrooke	Saint-François	45°23’44’’N	71°52’50’’W	24
Quebec	Windsor	Saint-François	45°34’04’’N	72°00’23’’W	24
Invasive range					
Landes	Saubusse	Adour	43°39’22’’N	01°11’13’’W	10
Landes	Riviere-Saas-et-Gourby	Adour	43°40’29’’N	01°08’06’’W	10
Landes	Pontonx-sur-l'Adour	Adour	43°47’03’’N	00°55’30’’W	35
Gironde	Cestas	Eau Bourde	44°45’20’’N	00°40’49’’W	30
Gironde	Bruges	Les Jalles	44°54’13’’N	00°36’16’’W	30
Gironde	Moulon	Dordogne	44°51’30’’N	00°13’10’’W	19
Gironde	Castillon-la-Bataille	Dordogne	44°51’04’’N	00°02’16’’W	19
Gironde	St-Denis-de-Pile	Isle	44°59’34’’N	00°12’29’’W	22

Table 2. Generalized linear mixed models (GLMM) analyses of traits related to growth, gas exchange and leaf morphology, biomass and biomass allocation in eight native and eight invasive populations of *Acer negundo* along a nutrient gradient. *F* values are given for fixed effects, log likelihood ratios (LLR) are given for random effects. Statistically significant values ($P < 0.05$) are shown in bold, marginally significant values ($P < 0.1$) are shown in italic.

		Source of variation									
Traits		Nutrient		Range		Nutrient x range		Pop(range)		Nutrient x pop(range)	
	AIC	*F*	*P*	*F*	*P*	*F*	*P*	LLR	*P*	LLR	*P*
Growth											
Diameter (mm)	5237.0	55.93	**<.0001**	5.92	**0.0289**	0.14	0.8718	12.3	**0.0004**	2.9	*0.0885*
Height (cm)	11004.7	39.43	**<.0001**	39.33	**<.0001**	2.37	0.1123	5.3	**0.0213**	4.2	**0.0404**
Leaf traits											
A_{area} (µmol CO$_2$.m^{-2}.s^{-1})	784.7	38.09	**<.0001**	0.04	0.8392	0.00	0.9980	2.7	0.1003	5.2	**0.0226**
A_{mass} (µmol CO$_2$.g^{-1}.s^{-1})	-467.9	31.78	**<.0001**	0.06	0.8098	0.24	0.7876	0.3	0.5839	0.9	0.3428
N$_{\mathrm{area}}$ (g N.m^{-2})	1.9	116.61	**<.0001**	28.96	**<.0001**	2.95	*0.0543*	0.0	1	0.0	1
N$_{\mathrm{mass}}$ (%)	486.0	194.18	**<.0001**	7.58	**0.0087**	0.13	0.8772	0.5	0.4795	2.8	*0.0943*
PNUE (µmol CO$_2$.g^{-1} N.s^{-1})	929.2	17.91	**<.0001**	2.86	0.1135	0.03	0.9748	2.8	*0.0943*	0.6	0.4386
LMA (g.m^{-2})	2032.0	0.97	0.4069	8.94	**0.0098**	0.10	0.9087	0.7	0.4028	1.1	0.2943
L$_{\mathrm{s}}$ (cm^2)	2343.6	14.44	**<.0001**	20.21	**0.0005**	0.31	0.7393	0.8	0.3711	0.2	0.6547
Biomass											
W_{t} (g)	2590.9	17.06	**<.0001**	0.02	0.8985	0.23	0.7928	0.0	1	0.9	0.3428
W_{a} (g)	2454.3	18.93	**0.0002**	1.24	0.2709	0.25	0.7803	0.0	1	1.5	0.2207
W_{l} (g)	1559.5	37.29	**<.0001**	0.16	0.6915	0.11	0.8944	0.0	1	1.0	0.3173
W_{s} (g)	2338.2	14.51	**0.0006**	1.60	0.2132	0.35	0.7099	0.0	1	1.5	0.2207
W_{r} (g)	1886.0	9.47	**0.0001**	10.74	**0.0059**	0.24	0.7837	0.0	1	1.1	0.2943
A_{l} (m^2)	-609.1	14.42	**0.0012**	5.62	**0.0326**	1.45	0.2355	1.3	0.2542	0.5	0.4795
Biomass allocation											
RSR (g.g^{-1})	-308.2	20.25	**<.0001**	54.33	**<.0001**	0.38	0.6846	0.7	0.4028	3.0	*0.0833*
LWR (g leaf.g^{-1} plant)	-1011.7	32.35	**<.0001**	5.32	**0.0277**	1.74	0.1893	0.7	0.4028	0.7	0.4028
SWR (g stem.g^{-1} plant)	-772.7	0.06	0.9401	66.33	**<.0001**	2.43	0.1068	1.6	0.2060	4.2	**0.0404**
RWR (g root.g^{-1} plant)	-705.8	17.63	**<.0001**	53.89	**<.0001**	0.11	0.8943	1.3	0.2542	3.7	*0.0544*
LAR (m^2 leaf.g^{-1} leaf)	-2577.3	29.76	**<.0001**	9.40	**0.0083**	0.79	0.4631	0.1	0.7518	2.9	*0.0886*

Table 3. Relative Distance Plasticity Index (RDPI) along a nutrient gradient for populations of *Acer negundo* from the native and invasive ranges. Comparisons of RDPI using a Generalized Linear Mixed Model with range as a fixed factor and population nested within range as a random factor. Significant difference between ranges ($P < 0.05$) denoted by an asterisk. See text for definition of terms.

Traits	RDPI low-to-medium nutrient levels		RDPI medium-to-high nutrient levels	
	Invasive	Native	Invasive	Native
Growth				
Height	0.12 ± 0.02	0.10 ± 0.02	0.04 ± 0.01	0.05 ± 0.01
Diameter	0.08 ± 0.01	0.07 ± 0.01	0.04 ± 0.01	0.04 ± 0.01
Leaf traits				
A_{area}	0.29 ± 0.04	0.28 ± 0.04	0.19 ± 0.03	0.14 ± 0.04
A_{mass}	0.24 ± 0.04	0.25 ± 0.06	0.15 ± 0.03	0.11 ± 0.03
$\mathrm{N}_{\mathrm{area}}$	0.24 ± 0.03	0.22 ± 0.02	0.27 ± 0.02	0.28 ± 0.04
$\mathrm{N}_{\mathrm{mass}}$	0.20 ± 0.04	0.19 ± 0.03	0.27 ± 0.02	0.25 ± 0.03
PNUE	0.11 ± 0.04	0.14 ± 0.04	0.21 ± 0.05	0.22 ± 0.04
LMA	0.06 ± 0.02	0.09 ± 0.02	0.03 ± 0.01	0.10 ± 0.02*
L_{s}	0.11 ± 0.01	0.07 ± 0.03	0.11 ± 0.03	0.08 ± 0.02
Biomass				
W_{t}	0.23 ± 0.04	0.26 ± 0.06	0.08 ± 0.02	0.14 ± 0.04
W_{a}	0.24 ± 0.04	0.28 ± 0.07	0.09 ± 0.03	0.15 ± 0.05
W_{l}	0.28 ± 0.06	0.31 ± 0.08	0.12 ± 0.04	0.15 ± 0.04
W_{s}	0.23 ± 0.04	0.28 ± 0.07	0.09 ± 0.02	0.16 ± 0.05
W_{r}	0.21 ± 0.05	0.20 ± 0.05	0.09 ± 0.04	0.11 ± 0.03
A_{l}	0.27 ± 0.06	0.28 ± 0.08	0.11 ± 0.03	0.10 ± 0.02
Biomass allocation				
RSR	0.15 ± 0.03	0.12 ± 0.04	0.09 ± 0.03	0.10 ± 0.01
LWR	0.11 ± 0.04	0.09 ± 0.02	0.08 ± 0.04	0.06 ± 0.04
SWR	0.04 ± 0.01	0.04 ± 0.01	0.02 ± 0.01	0.03 ± 0.01
RWR	0.11 ± 0.02	0.09 ± 0.03	0.07 ± 0.02	0.07 ± 0.01
LAR	0.13 ± 0.04	0.13 ± 0.03	0.12 ± 0.03	0.16 ± 0.03

Table 4. Plasticity Index (PI; Valladares et al. 2000) along a nutrient gradient for populations of *Acer negundo* from the native and invasive ranges. Comparisons of PI using a Generalized Linear Mixed Model with range as a fixed factor and population nested within range as a random factor. See text for definition of terms.

Traits	PI low-to-medium nutrient levels		PI medium-to-high nutrient levels	
	Invasive	Native	Invasive	Native
Growth				
Height	-0.22 ± 0.03	-0.17 ± 0.03	-0.04 ± 0.03	-0.01 ± 0.04
Diameter	-0.14 ± 0.02	-0.13 ± 0.02	-0.06 ± 0.03	-0.07 ± 0.02
Leaf traits				
A_{area}	-0.44 ± 0.04	-0.43 ± 0.05	-0.14 ± 0.11	-0.14 ± 0.09
A_{mass}	-0.38 ± 0.04	-0.38 ± 0.09	-0.13 ± 0.10	-0.07 ± 0.08
N_{area}	-0.38 ± 0.03	-0.35 ± 0.03	-0.43 ± 0.02	-0.43 ± 0.05
N_{mass}	-0.31 ± 0.07	-0.32 ± 0.05	-0.43 ± 0.02	-0.39 ± 0.04
PNUE	-0.14 ± 0.07	-0.17 ± 0.09	0.33 ± 0.07	0.35 ± 0.06
LMA	-0.06 ± 0.05	-0.02 ± 0.07	0.01 ± 0.03	-0.02 ± 0.08
L_{s}	-0.12 ± 0.06	-0.08 ± 0.07	-0.17 ± 0.05	-0.09 ± 0.05
Biomass				
W_{t}	-0.30 ± 0.09	-0.35 ± 0.10	-0.07 ± 0.06	-0.07 ± 0.10
W_{a}	-0.32 ± 0.10	-0.39 ± 0.09	-0.10 ± 0.06	-0.10 ± 0.11
W_{l}	-0.40 ± 0.08	-0.43 ± 0.08	-0.21 ± 0.06	-0.13 ± 0.10
W_{s}	-0.29 ± 0.10	-0.37 ± 0.10	-0.07 ± 0.06	-0.09 ± 0.12
W_{r}	-0.23 ± 0.11	-0.28 ± 0.09	-0.01 ± 0.08	0.00 ± 0.08
A_{l}	-0.40 ± 0.08	-0.39 ± 0.09	-0.18 ± 0.06	-0.13 ± 0.05
Biomass allocation				
RSR	0.14 ± 0.09	0.20 ± 0.06	0.09 ± 0.06	0.11 ± 0.06
LWR	-0.18 ± 0.06	-0.17 ± 0.03	-0.13 ± 0.04	-0.06 ± 0.04
SWR	0.00 ± 0.03	-0.05 ± 0.03	0.01 ± 0.02	-0.02 ± 0.03
RWR	0.12 ± 0.07	0.14 ± 0.05	0.06 ± 0.05	0.07 ± 0.04
LAR	-0.12 ± 0.09	-0.12 ± 0.08	-0.15 ± 0.07	-0.03 ± 0.11

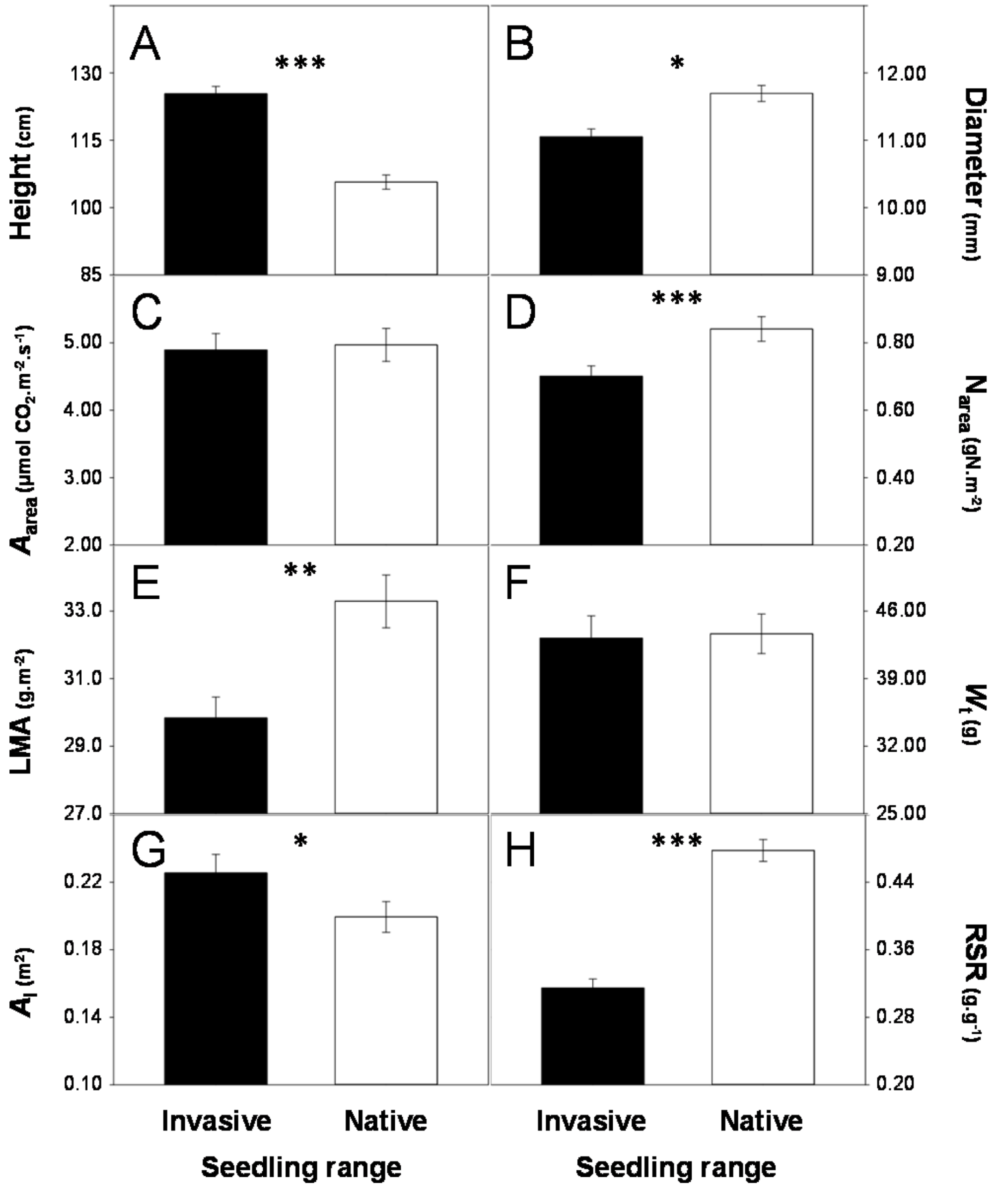

Fig. 1. Means ± SE of life-history traits for native and invasive seedlings of *Acer negundo*. Differences in growth (A,B), physiology (C,D), leaf morphology (E), biomass (F,G) and biomass allocation (H) were calculated across nutrient levels. n = 576 (height and diameter), 96 (A_{area}) and 144 (N_{area}, LMA, W_t and A_l) per range. See text for definition of terms. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

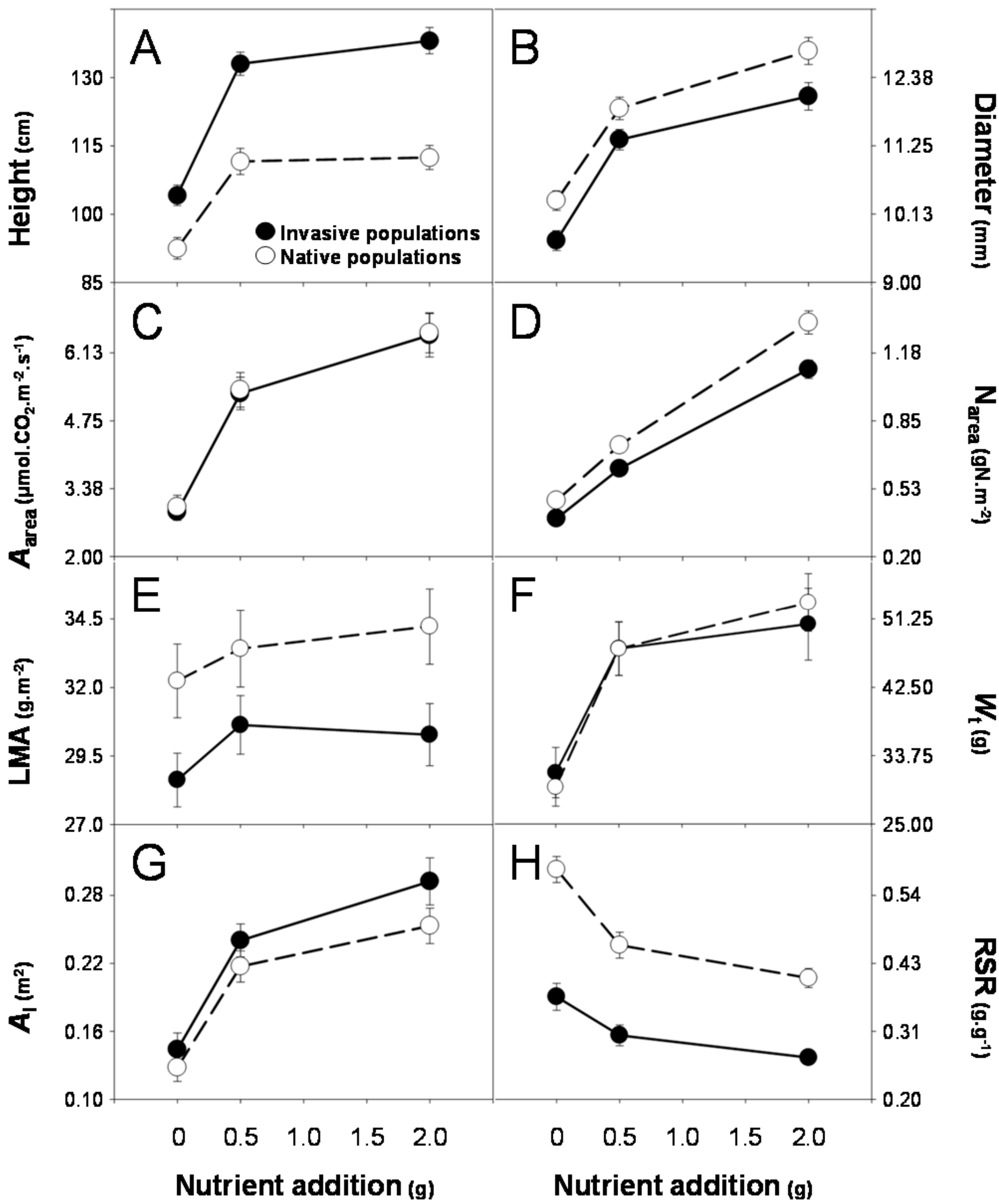

Fig. 2. Plasticity of native and invasive seedlings of *Acer negundo* to nutrient availability. Means ± SE of traits related to growth (A,B), physiology (C,D), leaf morphology (E), biomass (F,G) and biomass allocation (H) are represented. n = 192 (height and diameter), 32 (A_{area}) and 48 (N_{area}, LMA, W_t and A_l) per range and nutrient level. See text for definition of terms.

Synthesis

Theory

This project examined the ecological and evolutionary processes that drive the spread of *Acer negundo* and *Acer platanoides* in their introduced ranges. The following predictions were tested:

(*i*) Population size and density of invasive species are greater in their introduced than in their native range. A total of 136 forests were visited in Southern France and Southern Ontario, Canada in order to estimate the current local and regional extent of maple tree invasion and evaluate impacts on native communities (Chapter 1).

(*ii*) Environmental conditions (*i.e.* habitat invasibility) and functional traits (*i.e.* species invasiveness) contribute synergistically to the success of invasive species. To identify specific abiotic factors and traits that favor maple tree invasion, performances of invasive *A. negundo* and co-occurring native tree species seedlings were compared in response to environmental gradients (light and nutrient availability; Chapter 2). Meta-analyses were also conducted to search for general patterns among the tree invasion literature (Chapter 3).

(*iii*) Phenotypic plasticity, pre-adaptation and post-introduction evolution of functional traits are different mechanisms which allow exotic species to outcompete native species and thus to persist and spread under variable conditions in their introduced ranges. The importance of these sources of phenotypic variation in the success of exotic maple trees was studied using a quantitative genetic approach, *i.e.* by comparing performance-related traits between native and invasive genotypes growing in common gardens (Chapters 4 and 5).

Gurevitch et al. (2011) proposed a conceptual framework to unify principles of ecology and evolutionary biology and facilitate the consideration of the many ways in which these processes can promote invasions (see Fig. 2 of the Introduction). This mechanistic framework was used as a tool for synthesizing the findings obtained in each of the two cases of maple tree invasion.

Summary of major findings

Quantitative comparisons of population demography between native and introduced ranges revealed differences in pattern of invasion between *Acer negundo* and *Acer platanoides*, at least throughout the geographical areas we focused on (Table 1). At this point in time, *A. platanoides* is present but not yet locally dominant in forests of Southern Ontario (Chapter 1). Introduced populations are not occurring at higher density or abundance than populations from the native range, and are not affecting abundance of co-occurring native tree species. The proportion of well-established populations is also regionally limited. These findings contrast with previous observational work that showed a significant local and regional dominance in deciduous forests of northeastern U.S. (Martin 1999; Bertin et al. 2005; Fang 2005). The pattern of invasion differs for *A. negundo*, which has already aggressively invaded riparian habitats of Southern France. Introduced populations have reached higher density than native populations. They are also extensively distributed at the regional level, and significantly reduce native species abundance (Chapter 1). This is in line with recent studies that indicated the occurrence of *A. negundo* monodominant stands in many floodplain forests of Southern and Eastern Europe (Protopopova et al. 2006; Saccone et al. 2010; Gonzalez-Munoz et al. 2011; Pysek et al. 2012).

Invasive seedlings of *A. negundo* outcompeted native tree individuals under non-limiting conditions of light and nutrients (Chapter 2; Table 1, Fig. 1). The idea that invasive species may gain from high resource availability was confirmed by the analysis of the main invasion hypotheses tested on invasive tree species. The fluctuating resource availability (FRA) and disturbance (D) hypotheses were supported by 23 of the 24 studies that tested them on different cases of tree invasion (Chaneton et al. 2004; Peperkorn et al. 2005; Schumacher et al. 2009) (Chapter 3; Table 1). Fertilization, nutrient loading, canopy removal and forest fragmentation therefore represent conditions that are more likely to facilitate invasion by exotic tree species. However, successful invasion also requires that exotic species possess relevant traits that would allow them to perform better than native species under high-resource conditions. In this regard, the meta-analysis conducted on functional traits of invasive trees provided interesting insights. Although plant biomass, density/cover, germination and survival predict well the success of invasive trees, growth rate is the most relevant trait associated with tree invasiveness (Chapter 3). This result supports other global analyses that demonstrated higher growth rate values for invasive than non-invasive species (Pysek and Richardson 2007; van Kleunen et al. 2010). It also matches the findings of the interspecific comparison experiment that the competitive advantage of invasive *A. negundo* over native trees is explained by a higher growth rate via greater resource allocation to foliage in response to increased resource availability (Chapter 2).

Finally, our test of the genetic changes in invasive maple trees produced mixed results (Table 1). Seedlings of *A. platanoides* from native and invasive populations did not differ in any mean values of life-history traits and showed similar magnitude of plasticity across environmental conditions (home *vs.* away; Chapter 4; Fig. 2). In contrast, invasive seedlings of *A. negundo* performed better than their native conspecifics (Fig. 1). They grew significantly faster thanks to a greater allocation of resource to above-ground biomass, and also showed greater phenological sensitivity to increasing spring temperatures (Chapter 4). Invasive individuals of *A. negundo* may thus have undergone genetic shift towards higher competitive ability. Moreover, invasive *A. negundo* genotypes were similarly plastic than native *A. negundo* individuals (Chapter 5) but more plastic than co-occurring native species in response to nutrient availability (Chapter 2), which means that plasticity to nutrient gradient is probably pre-adapted in *A. negundo* (Fig. 1). Overall, it is likely that life-history traits are both genetically and environmentally determined in *A. negundo*, but only environmentally controlled in *A. platanoide*s.

Theoretical consequences

The observational and experimental studies of the project (Chapters 1, 3-5) supported both the findings of the systematic review and meta-analyses on tree invasions (Chapter 2) and the literature in general (Hierro et al. 2005; Catford et al. 2009), showing that invasions are complex processes synergistically driven by extrinsic abiotic conditions and intrinsic species traits. Increased nutrient and light availability following natural or anthropogenic disturbances interact with pre-adaptation and possible genetic evolution of functional traits to promote invasion of Southern France riparian forests by *A. negundo* (Fig. 1). Processes of invasion can also be influenced by residence time and propagule pressure (Gravuer et al. 2008; Eschtruth and Battles 2009), and these factors not tested here would thus merit further attention. Moreover, we found evidence that invasive species can at the same time possess pre-adaptations to novel conditions and undergo rapid post-evolution. Invasive individuals of *A.*

negundo exhibited pre-adapted higher levels of plasticity than native species in response to increased resource availability (*cf.* Master-of-some strategy; Richards et al. 2006) as well as genetically-based differences in growth and above-ground resource allocation compared to their native conspecifics. These results have implications for conservation issues. Pre-adaptation suggests that predicting invasiveness outcomes might be possible by comparing traits of genotypes considered for introduction with traits of already introduced ones (Schlaepfer et al. 2010) whilst the potential for post-introduction evolution implies that importation of new genotypes and gene flow among populations should be limited to reduce species adaptive potential (Dlugosh and Parker 2008).

Interestingly, the two studied maple tree species displayed different stage of invasion (Fig. 1 and 2). The early successional *A. negundo* is currently more dominant and established in riparian habitats across Southern France (*i.e.* more advanced stage of invasion) than the late-successional *A. platanoides* in inland deciduous forests of Southern Ontario, Canada. This discrepancy could in theory be due to all the various explanations discussed herein and promoting invasions, *i.e.* residence time, native distribution range size, propagule pressure, disturbance and species traits (Thuiller et al. 2006; Pysek et al. 2009a,b; Eschtruth and Battles 2011). However, the two species have large native distribution ranges allowing them to tolerate a wide range of climates, and similar introduction dates with multiple repeated introduction events (Appendix 1). The difference in stage of invasion between species is therefore unlikely due to these factors, but rather to the combination of different disturbance regimes between habitats and different life-history strategy between species. Frequent disturbances in riparian habitats have probably favored the establishment of the fast-growing and highly competitive *A. negundo* while less disturbed inland forests have impeded dominance by the shade tolerant and dispersal limited *A. platanoides*. These results finally support the idea that the relative importance of determinants of invasion vary according to the stage of invasion, with species traits being more important in more advanced stages (Kolar and Lodge 2002; Dietz and Edwards 2006; Pysek et al. 2009a).

Implications for methodology

This project successfully demonstrated the suitability of various approaches when studying processes that promote invasions by exotic species. Biogeographical local and regional contrasts of spatial patterns proved to be a reliable means to infer the invasion stage of exotic species at a point in time in a specific novel region. Given that invasions are not processes occurring at a single spatial scale (Hamilton et al. 2005), we recommend coupling comparisons of population demography at the local scale with surveys of species' presence at the regional scale in order to quickly identify species that perform better away *vs.* at home and to prioritize control efforts (Paynter et al. 2003). Moreover, examining not only population abundance but also their age structure is critical since studies recently showed that invasive species do not necessarily occur at higher abundance in their introduced than in their native ranges (Firn et al. 2011; Parker et al. 2013). Quantification of population age structure would also give insights for projecting population growth rate via matrix population models (Marco and Paez 2000; Sebert-Cuvillier et al. 2007). For all these reasons we can bewail the current paucity of such field surveys (Hierro et al. 2005; Hinz et al. 2012). The relative importance of seed bank dynamics and natural enemy release in the success of invasive maple trees would now benefit from using such biogeographical approach between native and invasive ranges. Ideally, the test of propagule pressure and enemy release hypotheses would be conducted over multiple years and across whole distribution ranges to avoid confounding effects of weather conditions specific to the study year and site, which has rarely been applied to date (A. Roques, *pers. comm.*).

Meta-analysis represents a powerful synthetic tool both to advance science and summarize research findings. It has been superseding narrative reviews by providing a more powerful way to rigorously test hypotheses, search for general patterns across a wide range of studies and species, and identify research gaps while accounting for heterogeneity among studies (*e.g.* differences in sample sizes) and publication bias (Gurevitch and Hedges 1999; Nakagawa and Poulin 2012; Lortie et al. 2013). This approach allowed us to find that there are specific traits promoting tree invasiveness under different circumstances (Chapter 2), which supports other meta-analyses and systematic reviews conducted on invasive plant species in general (Daehler 2003; Pysek and Richardson 2007; van Kleunen et al. 2010). This result has important implications as considering tree species attributes might help to predict future invasions.

We demonstrated that quantitative genetics is an appropriate approach to better understand evolutionary histories of invasive species. The use of reciprocal common gardens in native and introduced ranges of the two species was particularly important to properly assess the different sources of phenotypic variation such as genetic differentiation and phenotypic plasticity. The fact that native and invasive populations of *A. platanoides* significantly differed in leaf nitrogen content (N_{area})

and leaf mass per area index (LMA) but only in the native range (France) emphasizes possible errors of interpretation when collecting data in only one environment. Had we conducted the experiment only in France, we might have concluded that invasive populations had evolved towards more conservative leaf traits. The quantitative genetic approach can be even more powerful with the support of molecular analyses. The next step in the study of maple tree invasion is therefore the comparison of the genetic structure between populations from native and introduced ranges to differentiate between evolution in the new habitat (showing that the same starting population genetically diverged following colonization) and founder effects. In this regard, a total of 21 and 13 populations of *A. negundo* and *A. platanoides* have already been sampled across the whole distribution ranges in North America (Appendices 19 and 20). Another potential direction of work would be the study of population local adaptation, characterized by higher fitness of resident genotypes compared to genotypes from other habitats ('local *vs.* foreign' criterion; Kawecki and Ebert 2004), and generally investigated via the use of reciprocal transplant experiments or common gardens along environmental gradients (Ebeling et al. 2011; Alexander et al. 2012).

Implications for habitat conservation and invasive species management

Introduced populations of *A. negundo* have been invading riparian habitats of Southern France via increased phenotypic plasticity for allocation to foliage and growth in response to increased resource conditions, in particular increased nutrient availability (Chapter 2). Mechanical and chemical controls may thus be successful, as they have been for other invaders such as the invasive tree *Melaleuca* *quinquenervia* (Martin et al. 2010). However, they might not limit reinvasion of the species if N availability remains high. A long-term control of the species and restoration of native tree communities could rely on lowering N availability. Perry et al. (2010) have recently reviewed different management approaches for increasing N immobilization, and these include soil C addition, establishment of low-N plant species, burning, grazing, topsoil or biomass removal. Although there is to date little evidence that these practices would reduce invasion in forests (Cassidy et al. 2004; LeBauer and Treseder 2008), they could be alternative methods to decrease the proliferation of *A. negundo* and should merit further attention.

The biogeographical contrasts that were applied to assess local and regional patterns of *A. negundo* and *A. platanoides* invasion could be used to set up a compatible method of description and management of invasive species across administrative stakeholders and between invasions. Whilst research in invasion biology has progressed very rapidly over the last three decades, a recurring criticism of the discipline is the lack of a common framework for linking theory and management (Hulme et al. 2008). Because invasions do not follow administrative borders, extents of invasions are usually measured by different stakeholders, agencies and governments (Hulme 2009). Therefore, collection and availability of data strongly differ around the world (Pysek et al. 2008; Nunez and Pauchard 2010), and have led to significant delays before management action is taken (Simberloff 2009). Contrary to conservation science that has elaborated the efficient IUCN Red List to determine the threat status of species, listing efforts in invasion biology have focused on opinions (Lowe et al. 2000; Mace et al. 2008). Yet a more quantitative procedure would be helpful to facilitate comparisons of the state of invasions between regions and to assess past and anticipate future trends and biosecurity risks (McGeoch et al. 2010). For example, knowledge of whether a species is already present in the country and the current invasion status of its populations are important to determine what strategy and how much effort should be spent on management. A standardized set of metrics has consequently been proposed to describe the presence of exotic species in a specified introduced range (J.R.U. Wilson, *pers. comm.*). The authors suggest that this set of metrics should provide information on fundamental characteristics of invasions, *e.g.* status, abundance, spatial extent and impact (Wilson et al., *submitted*). These metrics would help assessing both success and failures of current management efforts and improving future initiatives, in particularly as shifts in species distributions in response to climate change are expected to be analogous to invasions (Caplat et al. 2013). Other aspects of invasions could also be incorporated in this standardized framework, in particular functional plant traits that have high value for risk assessments and trait-based restoration approaches (Funk et al. 2008; Hui et al. 2011; Caplat et al. 2012).

Effective policies and programs to manage invasive species would lastly benefit from a better understanding of invasion risk under global change. Research has indeed indicated that ongoing global change will affect the impacts of invasions on native and managed ecosystems (Bradley et al. 2010). Rising global temperatures, altered precipitation regimes, increased carbon dioxide and nitrogen deposition and changing magnitudes and durations of extreme weather events are likely to modify both distribution and prevalence of invasive species (Vila et al. 2007; Chuine et al. 2012). In this context, niche-based and process-based models have become increasingly popular for projecting potential ranges of species under both current and future environmental conditions and defining priority areas for conservation (Thuiller et al. 2005a,b; Morin et al. 2008). For instance, Kleinbauer et al. (2010), who simulated the future distribution of the highly invasive tree *Robinia pseudo-acacia* in Austria under various climatic change scenarios, found that temperature currently constraints the actual species' distribution and advocated the pressing implementation of management strategies for areas of conservation value with the greatest risk of invasion such as montaneous regions. The development of such accurate models relies on the availability of data on population distribution, species physiology and dispersal ability that are obtained via field and experimental studies at local and regional scales (Pattison and Mack 2008; Bradley et al. 2010). The information we accumulated in this project on population demography, ecophysiology and competitive ability of invasive maple trees may consequently represent an important starting point towards the prediction of their future distribution patterns in their introduced ranges.

Conclusion

Invasion biology contributes to a better understanding of ecological and evolutionary processes that govern species coexistence. This project illustrated the importance of using different methods and a biogeographical approach to identify interacting influence of multiple factors in the success of invasive species. The genetic changes observed in *A. negundo* such as the greater phenological plasticity of invasive genotypes to temperature suggest that introduced individuals of exotic trees have the potential to rapidly evolve and adapt to novel conditions. This supports the idea that tree species possess the evolutionary responses to match their new climates (Aitken et al. 2008; reviewed in Alberto et al. 2013). Invasive trees thus represent appropriate models to assess the migration rate of tree population (dispersal ability) and the role of adaptive plasticity and natural selection in the climate warming context (Chevin et al. 2010). Comparisons of evolutionary mechanisms at different locations of their introduced ranges would be particularly interesting to test the hypothesis that genotypes with colonizing attributes are favored at the leading edges where expansion occurs whilst genotypes that are more capable of resisting to drought and heat stress are selected at the rear edges (Kremer et al., *in press*).

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Table 1. Summary of findings from the study of invasive maple trees. Prediction results are presented via extent of significance (+++: $p < 0.0001$, 0: non-significant) and final outcome on tree invasion.

Methodology	Prediction	Response	*A. negundo*	*A. platanoides*	Outcome
CH1. Spatial pattern	Invasive populations are larger than native conspecifics	Relative abundance	+++	0	yes/no
	Invasive populations grow denser than native conspecifics	Density	+++	0	yes/no
	Invasive populations are well established regionally	Presence-absence	+++	0	yes
	Invasive populations impact native community	Native species density	+++	0	yes/no
CH2. Inv *vs.* nat species	Invasive species outcompete native species	Growth rate	+++		yes
		Physiology	0		no
		Leaf morphology	+++		yes
		Biomass	+++		yes
CH3. Meta-analysis	Several hypotheses explain tree invasion	Habitat invasibility			yes
		Species invasiveness			yes
	Traits are good predictors of tree invasiveness	Growth rate			yes
		Biomass			yes
		Density/Cover			yes
		Germination			yes
CH4. Quantitative genetics	Genetic differentiation between native and invasive genotypes	Survival	+++	0	yes/no
		Growth rate	+++	0	yes/no
		Phenology	+++	0	yes/no
		Physiology	0	0	no
		Leaf morphology	+++	0	yes/no
CH5. Quantitative genetics	Genetic differentiation between native and invasive genotypes	Growth rate	+++		yes
		Physiology	0		no
		Leaf morphology	+++		yes
		Biomass	+++		yes
	Invasive genotypes are more plastic than natives	Growth rate	0		no
		Physiology	0		no
		Leaf morphology	0		no
		Biomass	0		no

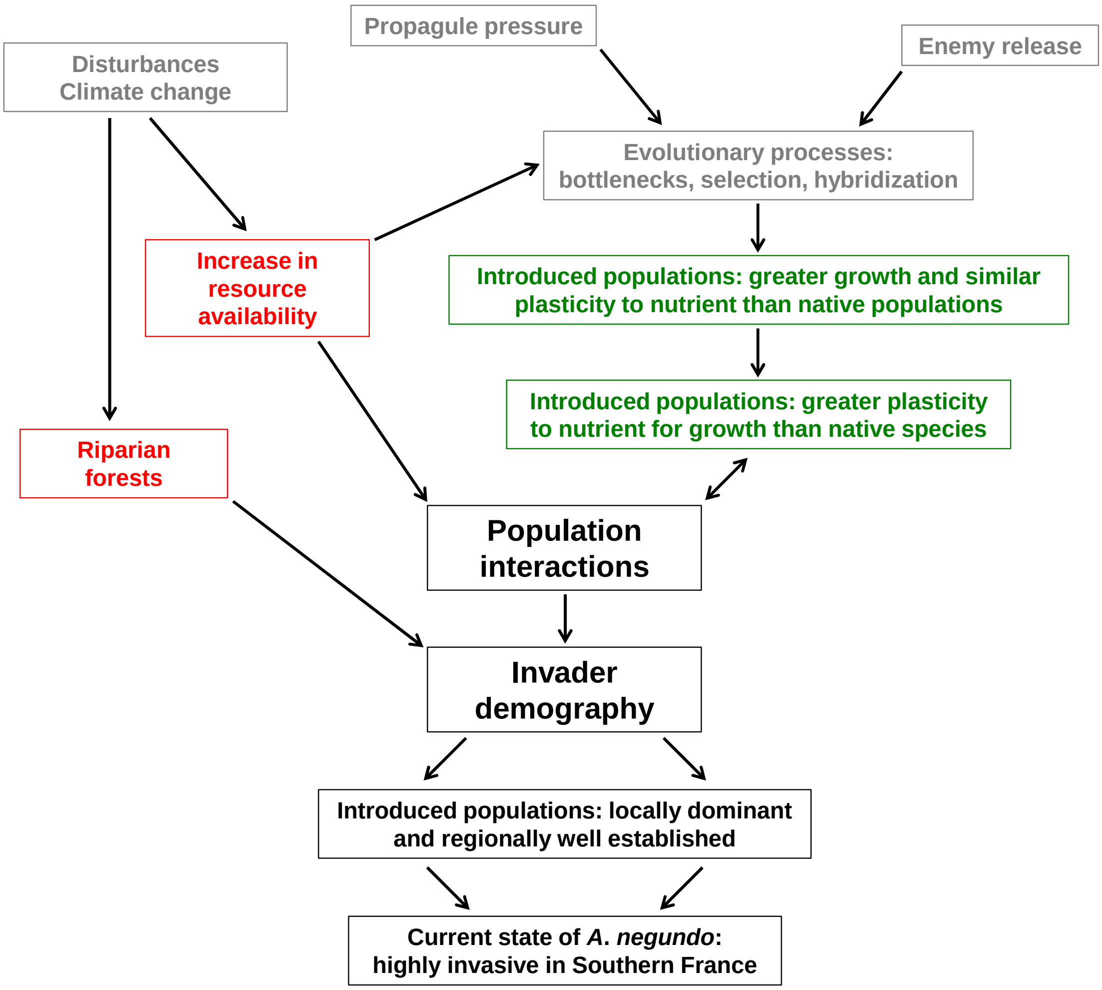

Fig. 1. Conceptual synthetic framework applied to *Acer negundo* invasion in Southern France. Abiotic and biotic characteristics are highlighted in red and green, respectively. Processes and states in grey are those that we did not study in this project.

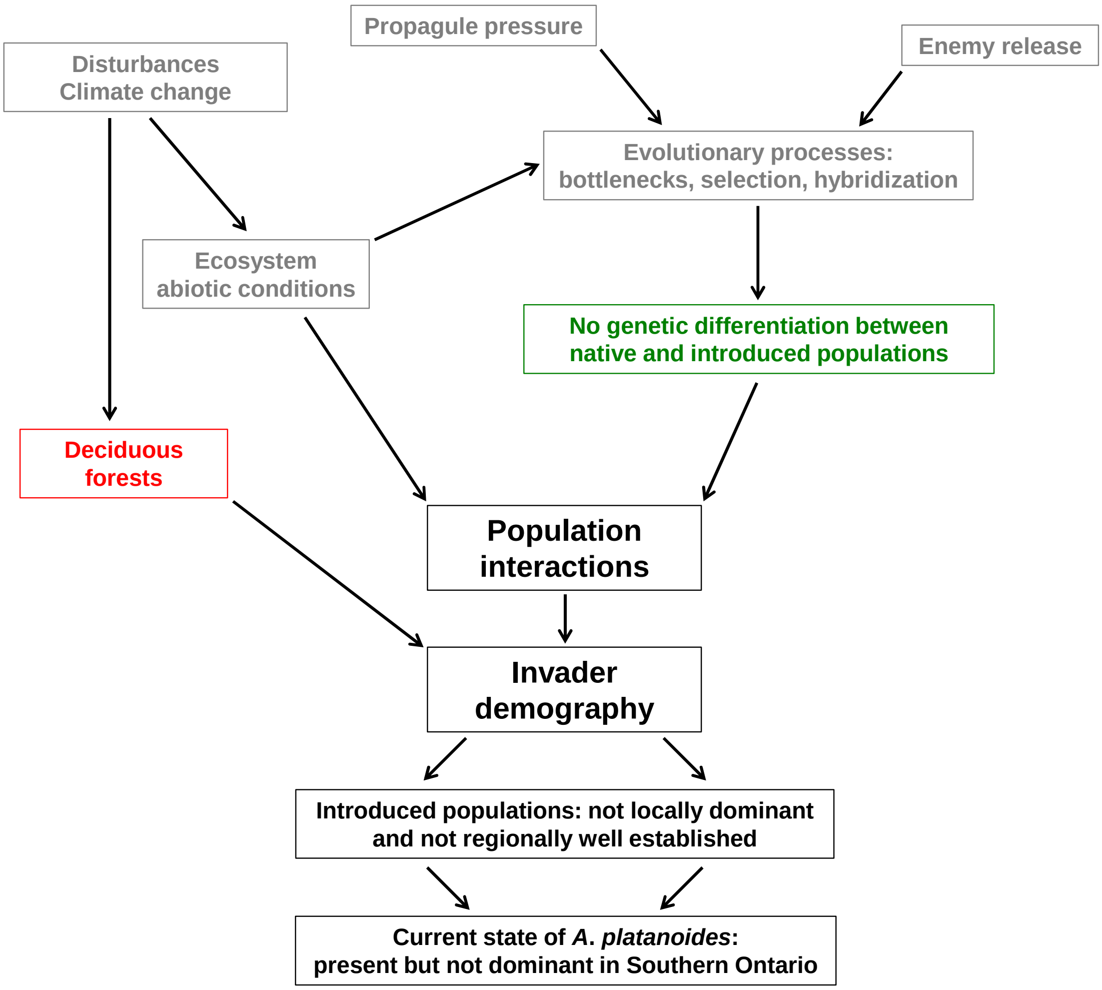

Fig. 2. Conceptual synthetic framework applied to *Acer platanoides* invasion in Southern Ontario, Canada. Abiotic and biotic characteristics are highlighted in red and green, respectively. Processes and states in grey are those that we did not study in this project.

Appendices

Appendix 1. Description of the two maple tree species studied in this project.

ACER NEGUNDO L.

Nomenclature

Order: Sapindales

Family: Sapindaceae (formerly Aceraceae)

Common names

North America: Box elder, Manitoba maple, Ash-leaved maple

France: érable negundo, érable a feuilles de frêne

Species identification

This deciduous short-lived species does not exceed 80 years of age with maximum age about 100 years (Rosario 1988). Individuals are medium sized trees up to 20 m in height and 1.2 m in diameter (Maeglin and Ohmann 1973). Their architecture is variable and depends on environmental conditions: they form upright trees with one trunk when growing in mesic forests with stable soil but their trunk can weep down when partially shaded like in forest edges (Medrzycki 2007). Young stems have a green to light grey bark that becomes darker and divided with irregular ridges in older individual (Rosario 1988). The root system is usually shallow but a short taproot with strong lateral toots can develop on deep soils (Maeglin and Ohmann 1973). *Acer negundo* is the only maple tree species with divided leaves, which are opposite with an unusual variable leaflet number: from 1 in juvenile to 5-7 in older trees (Rosario 1988; Medrzycki 2007). The species is considered as dioecious, windpollinated and protandrous but asexual reproduction by sprout and suckering is also common (Maeglin and Ohmann 1973; Wagner 1975; de Jong 1976). The age at first reproduction depends on resource availability: from as short as 5 years in open areas and at least moderate soil conditions to 15 years or more in forest understory (Medrzycki 2002). The flowering period begins in early spring before the development of leaves (Medrzycki 2007). Female seed crop is unusually high relative to other early-successional species and can potentially be affected by light availability (Schopmeyer 1974). The fruit is a winged paired samara occurring in drooping racemes and mature in autumn (Maeglin and Ohmann 1973).

Different varieties of this species occur naturally and are distinguished by morphological characteristics such as glaucousness, pubescence and color of branches and samaras as well as shape, size and number of leaflets per leaf (Dawson and Ehleringer 1993; Rosario 1988). These varieties include var. *negundo*, var. *interior*, var. *violaceum*, var. *texanum*, var. *californicum* and var. *arizonicum*.

Native range

Distribution

Acer negundo is native to North America where it is widely distributed (Maeglin and Ohmann 1973; Fig. 1). Its natural range of occurrence extends from southern Alberta and central Saskatchewan to southern Texas with local spots of occurrence in Mexico and Guatemala southward and from California to New England states and central Florida eastward. It has also been naturalized in Maine, southern Quebec, New Brunswick, Nova Scotia, Prince Edward Island and in southeastern Washington and eastern Oregon (Sargent 1965; Little 1971, 1979). It is generally dominant at mid-elevations but can be found at of 2300-2700 m of elevation in Mexico (Maeglin and Ohmann 1973; Ward et al. 2002). The different varieties are generally distributed as follows: var. *negundo* in eastern United States and introduced to eastern Oregon and Washington, var. *interior* from Rocky Mountains to Arizona and Canada, var. *violaceum* in northeastern United States and northern Great Plains, var. *texanum* in western Missouri, eastern Kansas and southeast United States, var. *californicum* in California and var. *arizonicum* in Arizona and New Mexico (Rosario 1988).

Fig. 1. Native range of *Acer negundo*. Illustration: Lamarque LJ (2013). Data sources: Rosario (1988) and the U.S. Geological Survey agency.

Ecology

Throughout its distribution range, this species is mostly confined in floodplains, riparian and palustrine communities (Ward et al. 2002; Dewine & Cooper 2008). However, it can also occur in dry coniferous forests, oak savannas and grasslands and colonize old fields and anthropogenic disturbed habitats (Rosario 1988; Medrzycki 2007). It grows on all types of soils from heavy clays to pure sands but prefers well-drained soils (Maeglin and Ohmann 1973; Rosario 1988). Establishment of *Acer negundo* is highly correlated to peak flow magnitude (DeWine and Cooper 2007) and the species is considered flood-tolerant with a 85-day survival threshold observed for inundation (Friedman and Auble 1999). It is less resistant than cottonwoods and willows but more tolerant than most of species from mesic forests, and consequently usually occurs in the upper floodplain terraces along big rivers (Everson and Boucher 1998). In the absence of flooding, it is successionally be replaced by more shade-tolerant species (Medrzycki 2007).

Although tolerating a wide range of conditions, this species is sensitive to water stress (Dina and Klikoff 1973 but see Dawson and Ehleringer 1993) with no evidence for xylem refilling following relief of soil drought (Hacke and Sperry 2003). It is highly vulnerable to cavitation with values of MCP (mean cavitation pressure) and P50 (50% loss of conductivity pressure) averaging -1.68 and -1.70 MPa, respectively (Lens et al. 2011). Like many dioecious species, *Acer negundo* also exhibits spatial segregation of the genders: females occur at high resource sites, i.e. in moist streamside habitats, whilst males dominate at low resource sites, i.e. in xeric and non-streamside habitats (Dawson and Ehleringer 1993). Such habitat-related sex ratio bias might be explained by differences in physiological responses with males expressing more conservative water-use patterns compared to females (Dawson and Ehleringer 1993; Ward et al. 2002; Dawson et al. 2004). For instance, females displayed higher mean sap flux density and mean canopy stomatal conductance per unit leaf area at the whole-plant level, although no difference between genders was found in branch hydraulic conductance and xylem cavitation vulnerability (Hultine et al. 2008). Interestingly, there is to date no evidence for difference in sex ratio between moist and dry sites in the introduced range (Medrzycki 2002; Erfmeier et al. 2011).

Acer negundo is fast-growing and generally considered a mid-successional species, although it can be a pioneer in some instances (Maeglin and Ohmann 1973). It is a component of various deciduous forest plant associations and often associated to overstory dominants such as cottonwoods (*Populus* spp.), willows (*Salix* spp.), American elm (*Ulmus americana*), black ash (*Fraxinus nigra*), pin oak (*Quercus palustris*) and bur oak (*Quercus macropcarpa*) (Maeglin and Ohmann 1973; Rosario 1988; Barbosa et al. 2000). This species has also been documented as a better competitor than exotic Tamarisk (*Tamarisk* sp.) and consequently suggested as a means to control Tamarisk invasion in riparian habitats of western United States (DeWine and Cooper 2008, 2010).

Finally, insect infestations are common and around 22 species of herbivores have been recorded feeding on this species (Tietz 1982 but see Jing and Coley 1990; Barbosa et al. 2000). Cottonwood (*Populus angustifolia* x *P. fremontii*) was found to suffer associational susceptibility to one of them, fall cankerworm (*Alsophila pometaria*), when growing under *Acer negundo* (White and Whitham 2000).

Introduced range

History of introduction

Together with several North American plant species, *Acer negundo* was intentionally imported in Europe during the seventeenth century (Medrzycki 2007). The earliest record is in Fulham Garden, England in 1688 (Kowarik 2003). Other introductions were first mentioned in 1690 for Holland, 1699 for Germany, 1808 for Poland, 1835 for Czech Republic and 1865 for Estonia (Pysek and Prach 2003; Medrzycki 2007). Admiral de la Galissonniere introduced the species in France in 1749 (Lair 1827; Williams 2008). In the second half of the nineteenth century, it became very popular due to its fast growth and was therefore widely used in horticulture and for landscaping purposes as a wind-break and shelterbelt tree (Tutin et al. 1968). It was also planted by bee-keepers because of its early pollen production in the spring and "Boxelder's honey" can be found in Bialowieza, Poland (Medrzycki 2007). Elsewhere, *Acer negundo* has also been planted in New Zealand where it is naturalized but not invasive and in southeastern Australia where it is considered invasive (Weber 2003).

Invasion of ecosystems

Acer negundo currently occurs in the same type of habitats than in its native range (Medrzycki 2007). It is mainly found in riparian forests characterized by high rate of flood disturbance and high soil nutrient level (Planty-Tabacchi et al. 1996; Tabacchi and Planty-Tabacchi 2003; Lamarque et al. 2012) where it forms monodominant stands at the ecotone between native softwood and hardwood communities (Pont 1999). It thus competes with species early successional species such as *Alnus* *glutinosa* L., *Populus nigra* L. and *Salix alba* L. and with late-successional species such as *Fraxinus angustifolia* Vahl. and *Fraxinus excelsior* L. It also grows along roadsides and in industrial wastelands or dry ruderal sites (Rothmaler 1984; Sanz Elorza et al. 2004).

Fig. 2. Invasive range of *Acer negundo*. Illustration: Lamarque LJ (2013). Data sources: DAISIE (Delivering Alien Invasive Species Inventories for Europe) and NOBANIS (The European Network on Invasive Alien Species) databases.

To date, this species is found in all European countries (DAISIE database http://www.europe-aliens.org) where it is globally rated as a species at high risk (Weber and Gut 2004). It is considered invasive in Spain, France, Germany, Czech Republic, Hungary, Poland, Ukraine, the Baltic States and Russia (Fig. 2; Kowarik 2003; Sanz Elorza et al. 2004; Protopopova et al. 2006; Medrzycki 2007; Csiszar

2009; Borisova 2010; Gonzalez-Munoz et al. 2011; Janusauskaite and Straigyte 2011; Pysek et al. 2012).

ACER PLATANOIDES L.

Nomenclature

Order: Sapindales

Family: Sapindaceae (formerly Aceraceae)

Common names

North America: Norway maple

France: érable plane

Species identification

Acer platanoides is a deciduous tree not exceeding 150-200 years and growing to 30 m in height and 1.90 m in diameter (Mayer 1980; Prentice and Helmisaari 1991). Individuals have a broad and rounded crown with a grey-brown bark that develops shallow and regular grooves with age (Chaney 1995). Leaves are opposite and palmately lobed with 5 to 7 lobes bearing few large teeth while the leaf petioles exude a white sap when broken (Rushforth 1999). This species is insect-pollinated and considered monoecious with heterodichogamous flowering, although it is also able to sprout (Prentice and Helmisaari 1991; Renner et al. 2007). Flowers, yellow-green and in corymbs of 15-30 together, appear early in the spring before emergence of new leaves (Rushforth 1999; Tal 2011). The fruit is a double samara with two-winged seeds and is wind-dispersed (Mitchell 1974; Greene and Johnson 1992 but see Rusanen et al. 2003). Seeds are shed dry and are dessication-tolerant (Finch-Savage et al. 1998). This species is reported to have prolific fecundity but does not produce viable seeds until 25-30 years of age (Mitchell 1974; Gordon and Rowe 1982 but see Wangen and Webster 2006).

It has been sparingly used as a timber species in Europe (Nowak and Rowntree 1990) whilst many cultivars have been selected for their distinctive leaf shapes or coloration, the most popular ones including ‘Columnare’, ‘Crimson King’, ‘Emerald Queen’, ‘Globosum’ and ‘Rubrum’ (Santamour and McArdle 1982; Conklin and Sellmer 2009).

Native range

Distribution

Acer platanoides is the most widespread native maple in Europe. It occurs from southern Scandinavia to northern Spain and Greece southward and from central France to the Ural Mountains, Asia Minor and northern Iran eastward (Fig. 3; Schmucker 1942). It is interestingly not naturally found in The Netherlands and The British Isles (Santamour and McArdle 1982). It occurs as far North as latitude 63°10’ in Sweden and is even found as a shrub at latitude 69°40’ in Norway (Nowak and Rowntree 1990). It usually grows up to 1250 m in the Alps and 1800 m in the Caucasus Mountains (Nowak and Rowntree 1990). It currently shows altitudinal and latitudinal upward shifts following climate warming (Kullman 2002).

Ecology

This dominant species of temperate forests mostly occurs in lowlands, *e.g.* in wide river valleys (Kostler 1956 but see Nowak and Rowntree 1990). It does not form pure stands over large areas but rather small groups in mixed forests and the genetic differentiation among populations is consequently high ($F_{st} = 0.099$; Eriksson et al. 2003; Rusanen et al. 2003). Its abundance in mixed stands and the size of its pure stands are greater in Central Europe than in Scandinavia (Nisbet 1893 but see Nowak and Rowntree 1990; Rusanen et al. 2003).

Fig. 3. Native range of *Acer platanoides*. Illustration: Lamarque LJ (2013). Data source: Nowak and Rowntree (1990).

Acer platanoides is a popular street tree in Europe because of its vigorous early growth rate, its wide site tolerances and its attractive dense canopy (Nowak and Rowntree 1990; Chaney 1995). It is however vulnerable to extreme heat and drought during seedling development (Kulagin et al. 1985). Overall, it grows best in areas with high amounts of precipitation and/or an underground supply of water (Mayer 1980) and prefers deep and fertile soils that are adequately drained with a pH of 5.5-6.5 (Loudon 1854 but see Nowak and Rowntree 1990). Accordingly, it was found to have an intermediate resistance to cavitation with values of MCP (mean cavitation pressure) and P50 (50% loss of conductivity pressure) averaging -2.29 and -1.91 MPa, respectively (Lens et al. 2011) whereas the sensitivity of xylem hydraulic conductivity to xylem sap ionic concentration might be adaptive in xeric and/or high light/temperature habitats (Nardini et al. 2012). In addition, *Acer platanoides* is also relatively shade-tolerant but requires more and more light for optimal growth when individuals mature (Prentice and Helmisaari 1991). Saplings increase their relative growth rate by investing more resources to leaf biomass rather than to net assimilation rate (Niinemets 1998). They constantly maintain a greater investment of biomass in leaves compared to standing biomass which increases their competitive ability in light-reduced environments (Niinemets 1998). Finally, along with *Fagus sylvatica* L. and *Acer pseudoplatanus* L., *Acer platanoides* has been a model system for investigating physiology, biochemistry and molecular biology of seed development, dormancy and dormancy breaking in tree species (Hong and Ellis 1990; Pinfield et al. 1992; Pawlowski 2010).

Introduced range

History of introduction

Acer platanoides was imported and cultivated in Great Britain at the Edinburgh Botanic Garden in 1683. It was first introduced to North America in 1756 by John

Bartram of Philadelphia, who had one of the two nurseries operating in the United States at that time (Nowak and Rowntree 1990). Another introduction of the species was made by William Hamilton circa 1784 (Spongberg 1990) whereas the earliest documentation of importation in California mentions 1861 (Nowak and Rowntree 1990). It was used as an ornamental street tree because of its desirable form and size as well as its tolerance to stressful urban environments (Nowak and Rowntree 1990) and was widely planted during the latter half of the twentieth century to replace *Ulmus americana* L. lost to Dutch elm disease (Wangen and Webster 2006).

Fig. 4. Invasive range of *Acer platanoides*. Illustration: Lamarque LJ (2013). Data sources: Munger (2003) and the U.S. Geological Survey agency.

Invasion of ecosystems

Acer platanoides can also tolerates a wide range of conditions in North America and grows particularly well on moist, moderately to well drained, fertile soils (Spongberg 1990; Lapointe and Brisson 2011). It thus invades riparian areas but also open lots as well as both interiors and fringes of urban forests (Webb and Kauzinger 1993; Reinhart et al. 2005; Martin and Marks 2006). It consequently competes with North American native species such as *Acer rubrum* L., *Acer saccharum* L., *Betula lenta* L., *Celtis occidentalis* L., *Fraxinus americana* L., *Prunus serotina* Ehrh., *Ulmus americana* L. and *Quercus* spp. (Martin 1999; Bertin et al. 2005; Fang 2005).

To date, *Acer platanoides* has been proliferating in the Northeast, eastern Midwest, the Northern Rocky Mountains and the Northwest of the United States as well as in eastern and southern Canada (Fig. 4; Nowak and Rowntree 1990; Gleason and Cronquist 1991; Munger 2003; Reinhart et al. 2005). It is specifically listed as a "noxious weed" by the U.S. federal government, as an invasive by the Connecticut state and a prohibited species by the Massachusetts state (USDA 2013 http://www.plants.usda.gov).

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Appendix 2. Key references of hypotheses proposed to explain the success of invasive species (classified by driving factor and hypothesis).

Propagule pressure

Propagule pressure (PP)

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

Sampling (SP)

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters 2: 140-148

Abiotic characteristics

Disturbance (D)

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10: 689-710

Dynamic equilibrium model (DE)

Huston MA (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Diversity and Distributions 10: 167-178

Empty niche (EN)

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

Environmental heterogeneity (EVH)

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, et al. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77-94

Fluctuating resource availability (FRA)

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

Habitat filtering (HF)

Melbourne BA, Cornell HV, Davies KF, Dugaw CJ, Elmendorf S, Freestone AL, Hall RJ, et al. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? Ecology Letters 10: 77-94

Opportunity windows (OW)

Johnstone, I.M. (1986) Plant invasion windows: a time-based classification of invasion potential. Biological Reviews 61: 369–394

Resource-enemy release (R-ER)

Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecology Letters 9: 887-895

Biotic characteristics

Adaptation (ADP)

Duncan RP, Williams PA (2002) Ecology - Darwin's naturalization hypothesis challenged. Nature 417: 608-609

Biotic indirect effects (BID)

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731-733

Biotic resistance (BR)

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7: 975-989

Darwin's naturalization (DN)

Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

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Enemy of my enemy (EE)

Eppinga MB, Rietkerk M, Dekker SC, De Ruiter PC, Van der Putten WH (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114: 168-176

Enemy inversion (EI)

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733

Evolution of increased competitive ability (EICA)

Blossey B, Nötzold R (1995) Evolution of Increased Competitive Ability in invasive nonindigenous plants - a hypothesis. Journal of Ecology 83: 887-889

Enemy release (ER)

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology & Evolution 17: 164-170

Enemy reduction (ERD)

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733

Facilitation (F)

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18: 119-125

Global competition (GC)

Alpert P (2006) The advantages and disadvantages of being introduced. Biological Invasions 8: 1523-1534

Invasional meltdown (IM)

Simberloff D, Holle BV (1999) Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions VI: 21–32

Increased susceptibility (IS)

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733

Ideal weed (IW)

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Limiting similarity (LS)

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802–804

Missed mutualisms (MM)

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, et al. (2006) Biotic interactions and plant invasions. Ecology Letters 9: 726-740

New associations (NAS)

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731-733

Novel weapons (NW)

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

Reckless invader (RI)

Simberloff D, Gibbons L (2004) Now you see them, now you don't! Population crashes of established introduced species. Biological Invasions 6:161–172

Specialist-generalist (SG)

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasion. Nature 427: 731-733

Appendix 3. Studies that tested invasion hypotheses on invasive tree species (classified by driving factor and hypothesis).

Propagule pressure

Propagule pressure (PP)

Barton AM, Brewster LB, Cox AN, Prentiss NK (2004) Non-indigenous woody invasive plants in a rural New England town. Biological Invasions 6: 205-211

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. Investigacion Agraria-Sistemas Y Recursos Forestales 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. Estuaries and Coasts 31: 960-968

Edward E, Munishi PKT, Hulme PE (2009) Relative roles of disturbance and propagule pressure on the invasion of humid tropical forest by *Cordia alliodora* (Boraginaceae) in Tanzania. Biotropica 41: 171-178

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

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

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

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

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

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

McGregor KF, Watt MS, Hulme PE, Duncan RP (2012) What determines pine naturalization: species traits, climate suitability or forestry use? Diversity and Distributions 18: 1013-1023

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. Journal of Ecology 95: 648-661

Nunez MA, Moretti A, Simberloff D (2011) Propagule pressure hypothesis not supported by an 80-year experiment on woody species invasion. Oikos 120: 1311-1316

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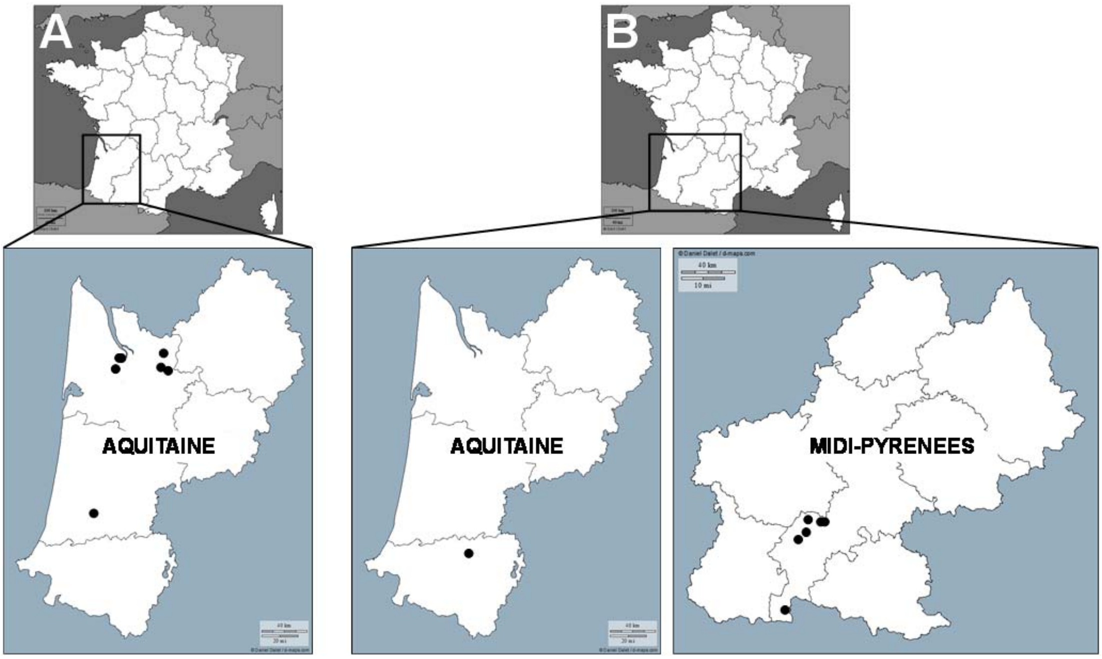
Appendix 4. Locations of *Acer negundo* populations sampled in the native and introduced regions for the demographic comparisons.

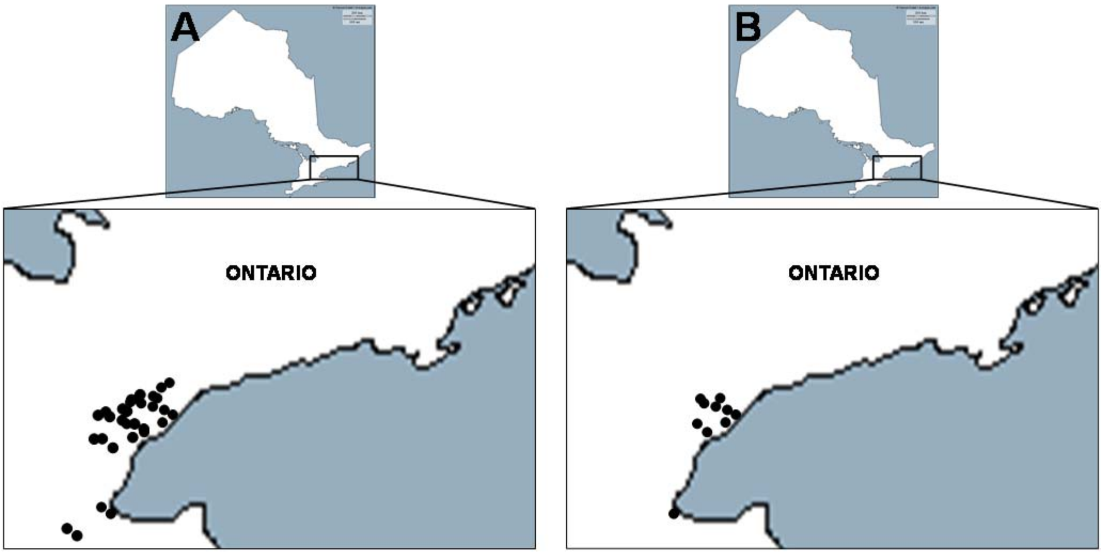
Range	Country	Region	Site	Elevation (m)	Latitude	Longitude	Habitat
Native	Canada	Ontario	Apple Creek Park	185	43°51'18.87" N	79°21'06.47" W	Maple/ ash woodland
Native	Canada	Ontario	Black Creek Trail	173	43°45'57.35" N	79°30'34.01" W	Maple/ ash woodland
Native	Canada	Ontario	Brickworks Park	83	43°40'43.24" N	79°22'12.97" W	Maple forest
Native	Canada	Ontario	Don East Parkland	136	43°46'57.11" N	79°22'19.43" W	Maple/ ash forest
Native	Canada	Ontario	Don Valley East	136	43°46'29.41" N	79°21'53.29" W	Maple/ ash forest
Native	Canada	Ontario	Don Valley West	163	43°45'40.57" N	79°26'12.48" W	Maple/ ash forest
Native	Canada	Ontario	Humber River	105	43°39'53.39" N	79°30'51.36" W	Maple/ ash woodland
Native	Canada	Ontario	King’s Mill Park	75	43°38'55.87" N	79°29'37.27" W	Maple woodland
Native	Canada	Ontario	G. Lord Ross Park	177	43°46'36.57" N	79°27'47.38" W	Maple woodland
Native	Canada	Ontario	Serena Gundy Park	121	43°43'05.53" N	79°21'34.98" W	Maple forest
Native	Canada	Ontario	Taylor Creek Park	112	43°42'01.49" N	79°18'19.15" W	Maple/ ash forest
Native	Canada	Ontario	West Deane Park	136	43°39'48.48" N	79°33'39.64" W	Maple woodland
Native	Canada	Ontario	Winfields Park	151	43°44'51.36" N	79°22'53.14" W	Maple/ ash woodland
Native	Canada	Ontario	King’s Forest Trail	105	43°13'02.10" N	79°48'15.71" W	Maple woodland
Native	Canada	Ontario	Ravine Road Trail	88	43°16'06.93" N	79°54'32.96" W	Maple/ ash forest
Native	Canada	Ontario	Toogood Park	179	43°52'25.74" N	79°19'16.91" W	Maple/ ash woodland
Introduced	France	Gironde	Bruges1	5	44°54'12.45" N	0°36'16.40" W	Poplar/ ash forest
Introduced	France	Gironde	Bruges2	6	44°54'22.69" N	0°36'25.84" W	Poplar/ ash forest
Introduced	France	Gironde	Cestas	37	44°45'20.37" N	0°40'49.95" W	Poplar/ willow woodland
Introduced	France	Gironde	Moulon	6	44°51'29.91" N	0°13'10.16" W	Ash forest
Introduced	France	Gironde	St-Jean-de-Blaignac	6	44°48'54.08" N	0°07'52.91" W	Poplar/ ash forest
Introduced	France	Gironde	St-Denis-de-Pile	5	44°59'35.66" N	0°12'28.45" W	Poplar/ willow woodland
Introduced	France	Landes	Pontonx-sur-l’Adour	14	43°47'05.57" N	0°55'23.76" W	Ash forest

Appendix 5. Locations of *Acer platanoides* populations sampled in the native and introduced regions for the demographic comparisons.

Range	Country	Region	Site	Elevation (m)	Latitude	Longitude	Habitat
Native	France	Haute-Garonne	Lilhac	372	43°17'49.35" N	0°49'33.07" E	Oak/ ash forest
Native	France	Haute-Garonne	Isle-en-Dodon	285	43°20'52.01" N	0°49'55.01" E	Oak/ ash forest
Native	France	Haute-Garonne	Sénarens	339	43°22'03.57" N	0°58'15.05" E	Oak/ ash forest
Native	France	Haute-Garonne	Luchon	876	42°44'41.89" N	0°36'30.87" E	Ash woodland
Native	France	Haute-Garonne	St-Lary-Boujean	343	43°13'25.67" N	0°44'53.31" E	Oak/ ash forest
Native	France	Haute-Garonne	Ambax	325	43°21'59.10" N	0°56'28.21" E	Oak/ ash forest
Native	France	Pyrénées-Atlantiques	Lacq-Audéjos	99	43°24'16.70" N	0°37'01.76" W	Oak/ ash forest
Introduced	Canada	Ontario	Brickworks Park	83	43°40'43.24" N	79°22'12.97" W	Maple forest
Introduced	Canada	Ontario	Don Valley East	136	43°46'29.41" N	79°21'53.29" W	Maple/ ash forest
Introduced	Canada	Ontario	Don Valley West	163	43°45'40.57" N	79°26'12.48" W	Maple/ ash forest
Introduced	Canada	Ontario	Humber River	105	43°39'53.39" N	79°30'51.36" W	Maple/ ash woodland
Introduced	Canada	Ontario	King’s Mill Park	75	43°38'55.87" N	79°29'37.27" W	Maple woodland
Introduced	Canada	Ontario	G. Lord Ross Park	177	43°46'36.57" N	79°27'47.38" W	Maple woodland
Introduced	Canada	Ontario	Serena Gundy Park	121	43°43'05.53" N	79°21'34.98" W	Maple forest
Introduced	Canada	Ontario	Taylor Creek Park	112	43°42'01.49" N	79°18'19.15" W	Maple/ ash forest
Introduced	Canada	Ontario	Winfields Park	151	43°44'51.36" N	79°22'53.14" W	Maple/ ash woodland
Introduced	Canada	Ontario	King’s Forest Trail	105	43°13'02.10" N	79°48'15.71" W	Maple woodland



Appendix 6. Populations of *Acer negundo* (A) and *Acer platanoides* (B) sampled in Aquitaine and Midi-Pyrénées, Southern France for the demographic comparisons



Appendix 7. Populations of *Acer negundo* (A) and *Acer platanoides* (B) sampled in Southern Ontario, Canada for the demographic comparisons.

Appendix 8. Overview of the 136 forests visited to assess the regional extent of invasion of *Acer negundo* and *Acer platanoides*, their habitat type (1 = isolated 10 ha urban/ suburban forest patch, 2 = isolated 10 ha rural forest) and degree of invasion (NO = uninvaded, INV = invaded, HIGH = highly invaded). Forests sampled were classified as uninvaded (species absent), moderately invaded (species present with up to 5 individuals, whatever life-stage) or highly invaded (population established with at least 15 adults).

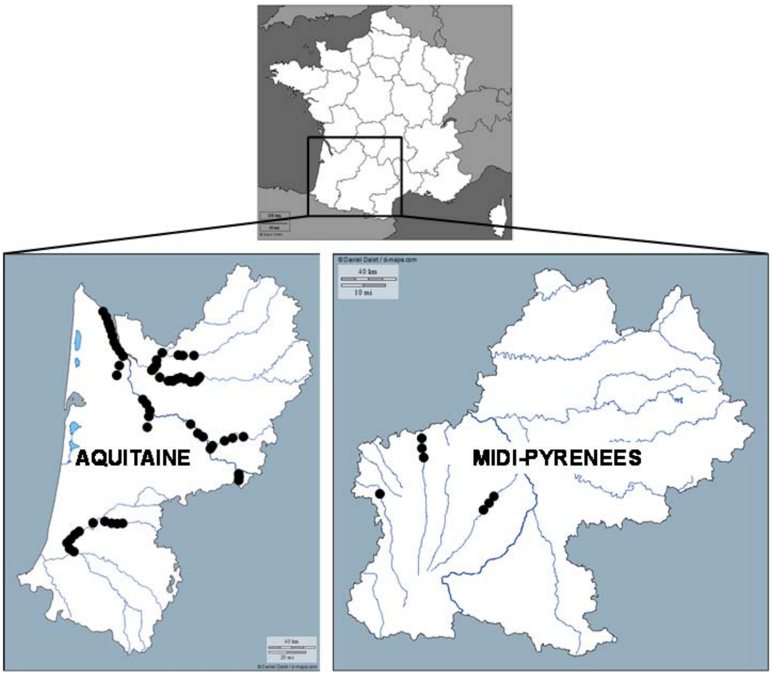
Species	Country	Region	Site	Latitude	Longitude	Habitat	Degree of invasion
A. negundo	France	Gironde	Macau	45°00'59.47" N	0°36'39.14" W	2	NO
A. negundo	France	Gironde	Labarde	45°01'38.55" N	0°37'31.80" W	2	NO
A. negundo	France	Gironde	Margaux	45°02'53.39" N	0°39'08.85" W	2	NO
A. negundo	France	Gironde	Soussans	45°04'05.00" N	0°40'04.09" W	2	NO
A. negundo	France	Gironde	Tayac	45°04'39.90" N	0°40'56.48" W	2	NO
A. negundo	France	Gironde	Lamarque	45°05'54.53" N	0°41'39.12" W	2	NO
A. negundo	France	Gironde	Cussan-Fort-Médoc	45°06'42.20" N	0°42'01.80" W	2	NO
A. negundo	France	Gironde	St-Julien-Beychevelle	45°09'56.05" N	0°43'46.61" W	2	NO
A. negundo	France	Gironde	Pauillac	45°12'04.84" N	0°44'54.79" W	2	NO
A. negundo	France	Gironde	St-Estèphe	45°16'02.71" N	0°45'31.09" W	2	NO
A. negundo	France	Gironde	St-Seurin-de-Cadourne	45°17'07.25" N	0°46'00.19" W	2	NO
A. negundo	France	Gironde	St-Yzans-Médoc	45°19'50.43" N	0°47'41.86" W	2	NO
A. negundo	France	Gironde	Queyzans	45°20'25.08" N	0°48'05.46" W	2	NO
A. negundo	France	Gironde	St-Christoly-Médoc	45°21'35.29" N	0°49'12.87" W	2	NO
A. negundo	France	Gironde	Langoiran	44°42'13.92" N	0°24'05.93" W	2	INV
A. negundo	France	Gironde	Podensac	44°39'21.75" N	0°21'20.54" W	2	INV
A. negundo	France	Gironde	Barsac	44°36'02.60" N	0°18'06.85" W	2	INV
A. negundo	France	Gironde	Pujols-sur-Ciron	44°33'31.43" N	0°21'20.61" W	2	INV
A. negundo	France	Gironde	Villandraut	44°27'32.49" N	0°22'05.07" W	1	INV
A. negundo	France	Gironde	Bruges	44°54'12.45" N	0°36'16.40" W	2	HIGH
A. negundo	France	Gironde	Cestas	44°45'20.37" N	0°40'49.95" W	1	INV
A. negundo	France	Gironde	Libourne	44°55'34.46" N	0°15'36.21" W	2	HIGH
A. negundo	France	Gironde	Arveyres	44°53'18.74" N	0°17'08.59" W	2	HIGH
A. negundo	France	Gironde	Moulon	44°51'29.91" N	0°13'10.16" W	2	HIGH
A. negundo	France	Gironde	Castillon-la-Bataille	44°51'05.17" N	0°02'16.32" W	1	HIGH
A. negundo	France	Gironde	St-Jean-de-Blaignac	44°48'54.08" N	0°07'52.91" W	2	HIGH
A. negundo	France	Gironde	Branne	44°49'56.09" N	0°11'00.70" W	2	HIGH

A. negundo	France	Gironde	Civrac-sur-Dordogne	44°49'50.99" N	0°04'55.89" W	2	INV
A. negundo	France	Gironde	Flaujagues	44°49'47.37" N	0°02'12.87" E	2	INV
A. negundo	France	Gironde	Eynesse	44°49'36.30" N	44°49'36.30" N	2	HIGH
A. negundo	France	Gironde	St-André-et-Appelles	44°49'10.46" N	0°11'29.81" E	2	HIGH
A. negundo	France	Gironde	Ste-Foy-la-Grande	44°50'26.90" N	0°12'35.58" E	1	HIGH
A. negundo	France	Gironde	Fronsac	44°55'11.75" N	0°16'27.21" W	2	INV
A. negundo	France	Gironde	St-Denis-de-Pile	44°59'35.66" N	0°12'28.45" W	2	HIGH
A. negundo	France	Gironde	Savignac-sur-l'Isle	44°59'13.19" N	0°13'58.94" W	2	INV
A. negundo	France	Gironde	Guîtres	45°02'17.66" N	0°11'10.51" W	2	INV
A. negundo	France	Gironde	St-Médard-de-Guizières	45°01'11.37" N	0°03'18.36" W	2	INV
A. negundo	France	Gironde	St-Seurin-sur-l'Isle	45°01'01.56" N	0°00'04.39" W	2	INV
A. negundo	France	Dordogne	St-Seurin-de-Prats	44°49'37.34" N	0°04'45.15" E	2	INV
A. negundo	France	Dordogne	Lamothe-Montravel	44°50'55.00" N	0°01'31.23" E	2	INV
A. negundo	France	Dordogne	Montpon-Ménestérol	45°00'37.83" N	0°09'43.65" E	2	INV
A. negundo	France	Lot-et-Garonne	Aiguillon	44°18'24.18" N	0°20'10.25" E	2	INV
A. negundo	France	Lot-et-Garonne	Clairac	44°21'28.25" N	0°22'39.22" E	2	INV
A. negundo	France	Lot-et-Garonne	Castelmoron-sur-Lot	44°23'42.35" N	0°29'39.54" E	1	HIGH
A. negundo	France	Lot-et-Garonne	Ste-Livrade-sur-Lot	44°24'05.38" N	0°35'12.31" E	1	INV
A. negundo	France	Lot-et-Garonne	Villeneuve-sur-Lot	44°25'03.82" N	0°41'52.24" E	1	INV
A. negundo	France	Lot-et-Garonne	Buzet-sur-Baïse	44°15'27.51" N	0°18'23.45" E	2	INV
A. negundo	France	Lot-et-Garonne	Lavardac	44°11'03.38" N	0°18'04.32" E	2	INV
A. negundo	France	Lot-et-Garonne	Nérac	44°07'53.36" N	0°20'33.94" E	1	INV
A. negundo	France	Lot-et-Garonne	Le Mas-d'Agenais	44°24'39.34" N	0°13'17.99" E	2	INV
A. negundo	France	Lot-et-Garonne	Marmande	44°29'55.72" N	0°09'15.60" E	1	INV
A. negundo	France	Lot-et-Garonne	Tonneins	44°23'17.07" N	0°18'04.86" E	1	INV
A. negundo	France	Gers	Condom	43°57'10.53" N	0°21'53.95" E	1	INV
A. negundo	France	Gers	Valence-sur-Baïse	43°52'34.45" N	0°23'00.47" E	2	INV
A. negundo	France	Gers	Beaucaire	43°50'14.10" N	0°23'10.15" E	2	INV
A. negundo	France	Gers	L'Isle-Jourdain	43°36'51.17" N	1°04'29.99" E	2	HIGH
A. negundo	France	Gers	Marestaing	43°34'35.76" N	1°01'24.82" E	2	HIGH
A. negundo	France	Gers	Cazaux-Savès	43°32'24.09" N	0°59'02.73" E	2	HIGH
A. negundo	France	Gers	Jû-Belloc	43°34'56.45" N	0°00'03.02" W	2	HIGH
A. negundo	France	Landes	Rivière	43°40'28.37" N	1°08'02.72" W	1	HIGH
A. negundo	France	Landes	Saubusse	43°39'20.82" N	1°11'15.13" W	2	HIGH

A. negundo	France	Landes	Tercis	43°41'27.30" N	1°05'34.43" W	2	HIGH
A. negundo	France	Landes	Pontonx-sur-l'Adour	43°47'05.57" N	0°55'23.76" W	1	HIGH
A. negundo	France	Landes	Josse	43°37'48.37" N	1°13'32.71" W	2	HIGH
A. negundo	France	Landes	Gouts	43°46'47.96" N	0°48'30.37" W	2	HIGH
A. negundo	France	Landes	Audon	43°47'16.40" N	0°49'32.68" W	2	HIGH
A. negundo	France	Landes	Onard	43°47'23.28" N	0°50'08.90" W	2	HIGH
A. negundo	France	Landes	Mugron	43°45'41.20" N	0°44'38.41" W	2	HIGH
A. negundo	France	Landes	Peyrehorade	43°32'36.50" N	1°07'03.27" W	2	INV
A. negundo	France	Landes	Ports-de-Lanne	43°33'58.32" N	1°11'30.12" W	2	INV
A. platanoides	Canada	Ontario	Aitken	43°52'36.20" N	79°19'02.35" W	1	NO
A. platanoides	Canada	Ontario	Apple Creek	43°51'18.37" N	79°21'06.47" W	1	INV
A. platanoides	Canada	Ontario	Ball Falls Park	43°07'56.04" N	79°22'48.01" W	2	INV
A. platanoides	Canada	Ontario	Battlefield Park	43°31'03.05" N	79°46'06.89" W	2	INV
A. platanoides	Canada	Ontario	Black Creek Trail	43°45'57.35" N	79°30'34.01" W	1	INV
A. platanoides	Canada	Ontario	Borer's Fall C. Area	43°17'03.72" N	79°55'46.40" W	2	NO
A. platanoides	Canada	Ontario	Brickworks Park	43°40'43.24" N	79°22'12.97" W	1	HIGH
A. platanoides	Canada	Ontario	Bronte Creek	43°25'12.01" N	79°45'56.50" W	2	NO
A. platanoides	Canada	Ontario	Bruce Creek	43°52'27.10" N	79°19'27.92" W	1	NO
A. platanoides	Canada	Ontario	Bruce Mill C.	43°56'46.14" N	79°21'07.97" W	2	NO
A. platanoides	Canada	Ontario	Christie Lake C. Area	43°16'54.51" N	80°01'41.47" W	2	NO
A. platanoides	Canada	Ontario	Colonel Danforth Park	43°46'50.60" N	79°10'32.73" W	1	HIGH
A. platanoides	Canada	Ontario	Crooks Hollow C. Area	43°16'36.69" N	80°00'01.05" W	2	NO
A. platanoides	Canada	Ontario	Devil's Punch Bowl	43°12'46.40" N	79°45'30.00" W	1	INV
A. platanoides	Canada	Ontario	Don East Parkland	43°46'57.11" N	79°22'19.43" W	1	INV
A. platanoides	Canada	Ontario	Don Valley East 1	43°46'29.41" N	79°21'53.29" W	1	INV
A. platanoides	Canada	Ontario	Don Valley East 2	43°48'20.30" N	79°22'17.00" W	1	INV
A. platanoides	Canada	Ontario	Don Valley East 3	43°47'52.40" N	79°22'53.70" W	1	INV
A. platanoides	Canada	Ontario	Don Valley West 1	43°45'40.57" N	79°26'12.48" W	1	INV
A. platanoides	Canada	Ontario	Don Valley West 2	43°45'13.80" N	79°25'39.00" W	1	HIGH
A. platanoides	Canada	Ontario	Dundas Valley C. Area	43°15'27.81" N	79°57'42.39" W	1	INV
A. platanoides	Canada	Ontario	Earl Bales Park	43°45'03.40" N	79°26'08.30" W	1	INV
A. platanoides	Canada	Ontario	Escarpment Trail	43°19'20.22" N	79°53'50.34" W	2	NO
A. platanoides	Canada	Ontario	Fairmount Park	43°13'11.24" N	79°45'45.88" W	1	INV
A. platanoides	Canada	Ontario	Finch East Greenbelt	43°46'54.70" N	79°22'34.20" W	1	INV

A. platanoides	Canada	Ontario	Forest Glade Walkway	43°28'12.37" N	79°41'16.72" W	1	NO
A. platanoides	Canada	Ontario	French Loyalist Park	43°54'42.10" N	79°27'18.31" W	1	NO
A. platanoides	Canada	Ontario	German Mills Park	43°48'51.28" N	79°22'33.97" W	1	INV
A. platanoides	Canada	Ontario	Ginger Valley	43°16'02.70" N	79°54'22.90" W	2	INV
A. platanoides	Canada	Ontario	Glen Rouge Park	43°48'25.80" N	79°08'16.70" W	1	INV
A. platanoides	Canada	Ontario	Glendale	43°12'48.85" N	79°47'46.43" W	1	INV
A. platanoides	Canada	Ontario	Highland Creek	43°45'42.96" N	79°12'04.99" W	1	HIGH
A. platanoides	Canada	Ontario	Humber River 1	43°39'22.70" N	79°30'00.20" W	1	INV
A. platanoides	Canada	Ontario	Humber River 2	43°39'39.11" N	79 30'08.12" W	1	INV
A. platanoides	Canada	Ontario	Humber River 3	43°39'43.70" N	79°30'38.60" W	1	INV
A. platanoides	Canada	Ontario	Humber River 4	43°39'53.39" N	79°30'51.36" W	1	INV
A. platanoides	Canada	Ontario	Humberwood Park	43°43'28.13" N	79°36'30.01" W	1	NO
A. platanoides	Canada	Ontario	Jordan Lions Park	43°09'01.37" N	79°21'49.02" W	2	INV
A. platanoides	Canada	Ontario	King's Mill Park	43°38'55.90" N	79°29'37.20" W	1	INV
A. platanoides	Canada	Ontario	King's Forest	43°13'02.01" N	79°48'15.70" W	1	INV
A. platanoides	Canada	Ontario	Lamoreaux Park	43°48'49.10" N	79°18'33.17" W	1	NO
A. platanoides	Canada	Ontario	Laurelwood Park	43°28'54.35" N	79°42'11.15" W	1	INV
A. platanoides	Canada	Ontario	Lions Valley Park 1	43°27'30.81" N	79°43'19.00" W	1	INV
A. platanoides	Canada	Ontario	Lions Valley Park 2	43°27'36.35" N	79°45'00.79" W	1	INV
A. platanoides	Canada	Ontario	Medway Valley Forest	43°00'55.02" N	81°18'12.82" W	1	NO
A. platanoides	Canada	Ontario	Milne Reserve	43°51'50.90" N	79°16'50.62" W	1	INV
A. platanoides	Canada	Ontario	Morningside Park	43°46'44.50" N	79°11'46.36" W	1	INV
A. platanoides	Canada	Ontario	Mud Street Park	43°11'45.97" N	79°47'20.09" W	2	NO
A. platanoides	Canada	Ontario	North Shore Trail	43°16'49.97" N	79°55'32.60" W	2	INV
A. platanoides	Canada	Ontario	Phyllis Rawlinson Park	43°55'15.97" N	79°23'48.63" W	1	NO
A. platanoides	Canada	Ontario	Ravencrest Park	43°39'35.19" N	79°33'33.22" W	1	INV
A. platanoides	Canada	Ontario	Red Hill Valley	43°13'17.80" N	79°47'47.87" W	1	INV
A. platanoides	Canada	Ontario	Rockaway Glen	43°08'15.33" N	79°18'32.22" W	2	INV
A. platanoides	Canada	Ontario	Rouge Valley Park	43°52'25.28" N	79°52'25.88" W	2	INV
A. platanoides	Canada	Ontario	Rowntree Mills Park	43°45'03.27" N	79°34' 22.62 W	1	INV
A. platanoides	Canada	Ontario	Serena Gundy Park	43°43'05.53" N	79°21'34.98" W	1	HIGH
A. platanoides	Canada	Ontario	Shangri-la Park	43°08'09.21" N	79°20'17.56" W	2	INV
A. platanoides	Canada	Ontario	Spencer Creek Trail	43°15'55.24" N	79°56'27.34" W	1	INV
A. platanoides	Canada	Ontario	Spencer Gorge W. Area	43°16'53.90" N	79°58'45.60" W	1	NO

A. platanoides	Canada	Ontario	Spring Creek C. Area	43°15'17.69" N	79°58'06.73'" W	2	NO
A. platanoides	Canada	Ontario	Sprucedale Park	43°01'34.56" N	81°15'11.18" W	1	NO
A. platanoides	Canada	Ontario	Taylor Creek Park 1	43°42'01.49" N	79°18'19.15" W	1	INV
A. platanoides	Canada	Ontario	Taylor Creek Park 2	43°42'05.80" N	79°19'11.20" W	1	INV
A. platanoides	Canada	Ontario	Thorpe Street	43°15'48.27" N	79°56'49.87" W	1	INV
A. platanoides	Canada	Ontario	Twickenham Park	43°53'28.29" N	79°27'45.82" W	1	HIGH
A. platanoides	Canada	Ontario	Winfields Park	43°44'51.36" N	79°22'53.14" W	1	INV



Appendix 9. Forests visited in Aquitaine and Midi-Pyrénées, Southern France to assess the regional extent of invasion of *Acer negundo*.

Appendix 10. Forests visited in Southern Ontario, Canada to assess the regional extent of invasion of *Acer platanoides*.

Appendix 11. Means and Tukey groups per species group for all measured traits and tested experimental conditions. For a given trait different letters on the same column indicate significant differences amongst species groups for a combination of light, fertilization and disturbance (Tukey test). Species are grouped by strategy: the invasive species is *Acer negundo*. Native early-successional species are *Salix alba* and *Populus nigra*, and native late-successional species are *Fraxinus excelsior* and *Fraxinus angustifolia*.

Tukey grouping		N+						N-					
		ND			D			ND			D		
Variables	Species	C	S	SS	C	S	SS	C	S	SS	C	S	SS
RGR_h	Invasive	7.22a	8.45a	0.52b	5.87a	7.68a	0.64b	2.23a	1.64b	0.73a	3.11a	1.55b	0.24a
	Early sc.	5.90a	6.80ab	5.81a	5.05ab	6.84a	4.15a	3.55a	3.8a	2.8a	3.34a	4.28a	3.16a
	Late sc.	3.43b	4.99b	2.91b	2.97b	4.54b	2.44ab	1.35a	1.69b	2.21a	1.72a	1.92b	1.51a
RSR	Invasive	0.42b	0.29b	0.51c	0.44b	0.32b	0.64b	0.73c	0.59b	0.72b	0.73b	0.86b	0.97b
	Early sc.	0.98a	0.90a	0.87b	0.93a	0.95a	1.22a	1.23b	1.36a	1.22a	1.17b	1.10b	1.06b
	Late sc.	1.11a	0.97a	1.27a	1.29a	0.99a	1.48a	1.93a	1.99a	1.36a	2.14a	2.08a	1.57a
TLA	Invasive	109.8a	160.1a	28.1a	63.4a	121.2a	23.1a	29.2a	32.3a	23.5a	20.9a	21.8a	9.5a
	Early sc.	37.8b	38.3b	23.3a	29.0b	42.6b	16.0a	14.1b	20.6b	17.0a	7.9b	15.8a	13.1a
	Late sc.	29.7b	62.0b	23.0a	18.2b	31.8b	17.0a	17.4b	16.6b	14.4a	5.9b	10.5a	13.2a
SLA	Invasive	31.19a	46.29a	53.05a	30.02a	42.74a	48.50a	30.02a	30.85a	48.54a	27.12a	46.36a	55.00a
	Early sc.	19.33b	23.03c	34.43c	17.04b	28.12b	36.37b	15.06c	24.01b	32.85b	17.58b	23.50b	33.70c
	Late sc.	19.82b	35.09b	45.10b	20.63b	35.64ab	43.26a	20.60b	31.02a	43.75a	18.52b	28.33b	43.81b
LWR	Invasive	0.37a	0.36a	0.28a	0.31a	0.35a	0.17a	0.21a	0.24a	0.21a	0.15a	0.16a	0.17a
	Early sc.	0.12b	0.14c	0.11b	0.12b	0.13b	0.07b	0.09c	0.09b	0.06c	0.06b	0.05c	0.06b
	Late sc.	0.19b	0.24b	0.17b	0.17b	0.18b	0.11b	0.14b	0.10b	0.14b	0.08b	0.10b	0.11b
A_{max}	Invasive	4.44a	5.78b		8.87a	5.33c		2.92b	2.03c		3.41b	4.98b	
	Early sc.	13.64a	15.35a		18.26a	15.04a		13.23a	11.55a		16.83a	13.86a	
	Late sc.	12.17a	9.38b		11.19a	9.95b		3.11b	5.64b		6.26b	7.51b	
A_{maxw}	Invasive	0.15a	0.13b		0.29a	0.13a		0.10a	0.07b		0.14b	0.13b	
	Early sc.	0.79a	0.66a		1.06a	0.58a		0.98a	0.49a		0.91a	0.66a	
	Late sc.	0.63a	0.28b		0.52a	0.30a		0.16a	0.19b		0.36b	0.28b	
N_m	Invasive	4.99ab	4.36a	3.94a	5.03a	5.19a	3.87a	1.23a	0.97c	2.21a	2.08a	2.2a	2.61a
	Early sc.	4.48b	4.11a	3.52ab	4.50a	4.01a	3.52ab	1.81a	2.49a	2.80a	2.67a	2.38a	2.56a

	Late sc.	5.24a	4.54a	2.93b	5.02a	4.66a	3.11b	1.67a	1.89b	2.30a	1.60a	1.77a	2.17a
PNUE	Invasive	2.92a	6.58a		5.46a	4.01b		7.23a	6.28b		6.19a	12.66a	
	Early sc.	6.33a	9.24a		7.66a	9.92a		11.25a	8.80a		13.78a	14.75a	
	Late sc.	4.34a	7.10a		5.28a	9.22b		5.16a	9.60a		7.42a	13.41a	
N_a	Invasive	1.60b	0.94b	0.74b	1.70b	1.22a	0.80a	0.41c	0.32c	0.46c	0.63b	0.48b	0.50b
	Early sc.	2.32ab	1.83a	1.03a	2.72a	1.47a	0.99a	1.21a	1.04a	0.73a	1.59a	1.02a	0.78a
	Late sc.	2.76a	1.34ab	0.65b	2.50a	1.27a	0.72a	0.81b	0.63b	0.52b	0.88b	0.65b	0.50b

RGR_h: relative height growth rate (mm. $mm^{-1}.d^{-1}.10^{-3}$), RSR: root shoot ratio (g. g^{-1}), TLA: total leaf area (m²), SLA: specific leaf area (m². kg^{-1}), LWR: leaf weight ratio (g. g^{-1}), A_{max}: light-saturated assimilation rate (µmol CO_2. m^{-2}. s^{-1}), N_m: nitrogen content (%), N_a: leaf nitrogen content (g. m^{-2}), PNUE: photosynthetic nitrogen use efficiency (µmol CO_2. g^{-1}N. s^{-1}). Environmental conditions are: Fertilised (N+), Non-fertilised (N-), Disturbed (D), Non-disturbed (ND), Full light (C), Shade (S) and Deep shade (SS).

Appendix 12. Control and treatment data for all the studies included in the meta-analysis conducted on the invasion hypotheses. Mean value, sample size and error term of both control and treatment were used to calculate Hedges'*d*.

Reference	Hyp.	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. (2010)	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
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 availabiity	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

Hyp.: hypothesis, 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 13. Control and treatment data for all the studies included in the meta-analysis conducted on the functional traits. Mean value, sample size and error term of both control and treatment were used to calculate Hedges'*d*.

Reference	Trait	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
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. (2010)	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, 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 availabiity	Invasive sp/ invasive population/ resource availability
Zou et al. (2008a)	B, Gr, S	Invasive sp/ native population/ resource availabiity	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

B: Biomass, Ge: Germination, Gr: Growth rate, DC: Density/ Cover, S: Survival.

Appendix 14. List of the invasive tree species studied in the 96 articles selected from the systematic review. 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.

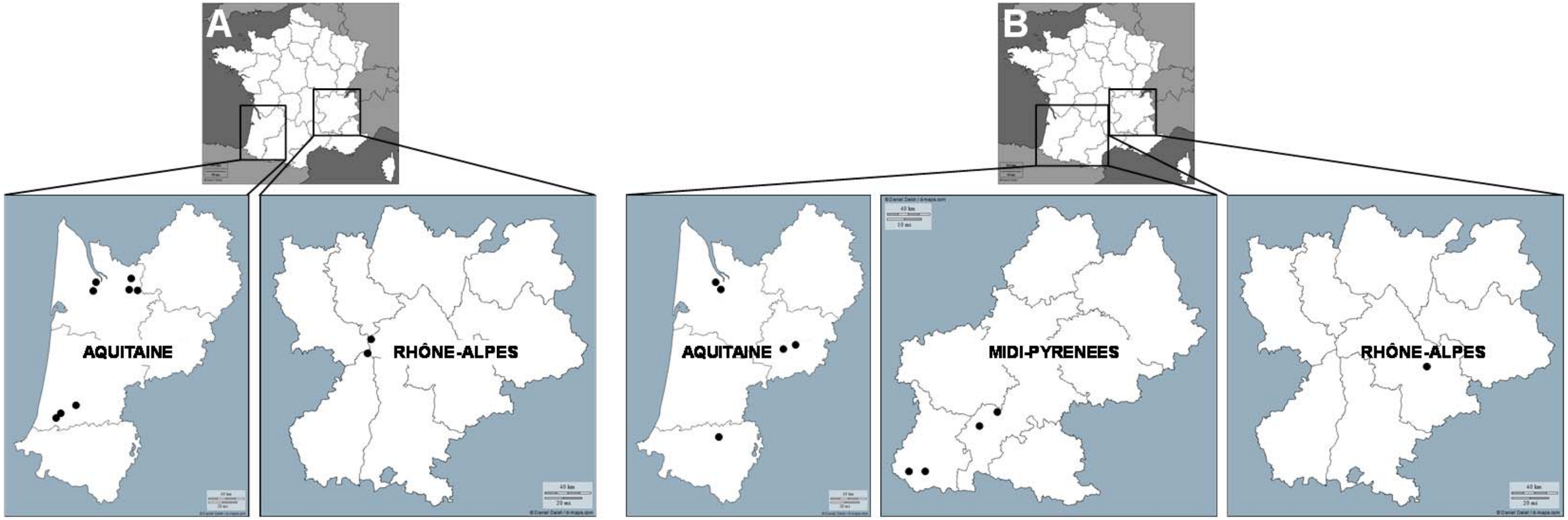
Invasive tree	Family	GrF	Native range		Introduced range		InvHab	Study location
			Location	Clim.	Location	Clim.		
A. cyclops	Mimosaceae	BE	S Aus, W Aus	T	SA	T	Sh	SA
A. dealbata	Mimosaceae	BE	SE Aus	T	S Eur	T	O, F	Spa
A. longifolia	Mimosaceae	BE	SE Aus	T	SA, Por	T	S, Sh, F	Por, Ger, SA
A. saligna	Mimosaceae	BE	SW Aus	T	SA	T	Sh, F	SA
Ac. negundo	Aceraceae	BD	N Am	T	Eur	T	D, R	USA, Fra, CZ
Ac. platanoides	Aceraceae	BD	Eur	T	NE Am	T	F	USA, Eur
Ad. pavonia	Fabaceae	BD	India, SE Asia	Tr	Ams, Pac Is	Tr	C, D, F	Aus
Ai. altissima	Simaroubaceae	BD	China	T/ STr	USA, SE Eur, Aus, NZ	T/ STr	D, O, F	USA, CZ
Al. macrophylla	Apocynaceae	BE	SE Asia	Tr	Ind Is, Pac Is	Tr	F	Seychelles
B. javanica	Euphorbiaceae	BE	SE Asia, Aus, Pac Is	Tr	Jap	STr	F	Jap
C. verum	Lauraceae	BE	Asia	Tr	Ind Is, Pac Is	Tr	F	Seychelles
E. angustifolia	Elaeagnaceae	BD	E Eur, Asia	T/ STr	S USA	T/ STr	F	USA
Er. japonica	Rosaceae	BE	SE Asia	T	N Am, Med Bas, SA	T	F	SA
Eu. uniflora	Myrtaceae	BE	Bra	Tr	SE USA	STr	F	USA
G. triacanthos	Fabaceae	BD	E N Am	T	Arg, Eur, SA, Aus	T	G, F	Arg
H. populifolius	Euphorbiaceae	BE	E Aus	T	SA, NZ, HI	T	F	SA
L. lucidum	Oleaceae	BE	E Asia	T	USA, Arg, S Af, Aus, NZ	T	G, F	Arg
M. quinquenervia	Myrtaceae	BE	E Aus, NGui, NCal	T/ STr	SE USA	STr	G, Sh, F	USA
P. lophantha	Fabaceae	BE	SW Aus	T	S Am, S Af, NZ, HI	T	F	SA
Pa. tomentosa	Scrophulariaceae	BD	Asia	T	USA	T	F	USA
Pi. canariensis	Pinaceae	C	Canary Is	T	W USA, SA, Aus	T	Sh, for	SA
Pi. halepensis	Pinaceae	C	Med Bas	T	S Am, S Af, Aus, NZ	T	G, Sh, F	Arg, SA
Pi. pinaster	Pinaceae	C	W Eur, N Af	T	SA	T	Sh, F	SA
Pi. ponderosa	Pinaceae	C	W NA	T	S Am, SA, Aus, NZ	T	G, Sh, F	Arg
Pi. radiata	Pinaceae	C	W NA	T	S Am, SA, Aus, NZ	T	G, Sh	Arg, SA
Pi. strobus	Pinaceae	C	NA	T	Eur, SA	T	G, Sh, F	CZ, SA

Pit. undulatum	Pittosporaceae	BE	SE Aus	STr	Car Is, S Bra, Az Is, SA	T/ STr	F	Jam, SA
Pop. x canescens	Salicaceae	BD	Eur	T	N Am, SH	T	F	SA
Pr. caldenia	Fabaceae	BE	S Am	T	Arg	T	G, F	Arg
Pn. serotina	Rosaceae	BD	N Am	T	Eur	T	G, F	USA, Fra, Bel, Hol, CZ, Pol,
Ps. menziesii	Pinaceae	C	W N Am	T	W Eur, SA	T	F	Arg
Pd. cattleianum	Myrtaceae	BE	S Am	Tr	Ind Is, Pac Is	Tr	F	Seychelles
Q. robur	Fagaceae	BD	Eur, N Af, W Asia	T	N Am, SA	T	F	SA
Q. rubra	Fagaceae	BD	E N Am	T	Eur	T	F	CZ
R. cathartica	Rhamnaceae	BD	Eur, W Asia	T	N Am	T	O, F	USA
Ro. pseudo-acacia	Fabaceae	BD	SE USA	T	Eur, S Af, Asia	T	D, F	USA, CZ, Jap
S. koetjape	Meliaceae	BE	SE Asia	Tr	Ind Is, Pac Is	Tr	F	Seychelles
Sa. sebiferum	Euphorbiaceae	BD	E China	T/ STr	SE USA	T/ STr	G, C	USA, China
Sc. molle	Anarcadiaceae	BE	S Am	A	S USA, SA, Aus	A	G, F	SA
Sc. terebinthifolius	Anarcadiaceae	BE	S Am	STr/ Tr	S USA, S Af, Ind Is, Pac Is	STr	G, F	USA
So. mauritianum	Solanaceae	BE	S Am	T/ Tr	S Af, Ind Is, Aus, NZ, Pac Is	T/ Tr	F	SA
Sy. jambos	Myrtaceae	BE	SE Asia	Tr	C Am, Ind Is, Aus, Pac Is	Tr	F	Seychelles
T. pallida	Bigogniaceae	BE	Lesser Antilles	Tr	Ind Is	Tr	F	Seychelles
Ta. ramosissima	Tamaricaceae	BD	E Eur, Asia	T	USA, Arg, SA, Aus	T	F	USA
U. pumila	Ulmaceae	BD	E Si, N China, Kor	T	USA, Mex, Arg	T	G, F	Arg

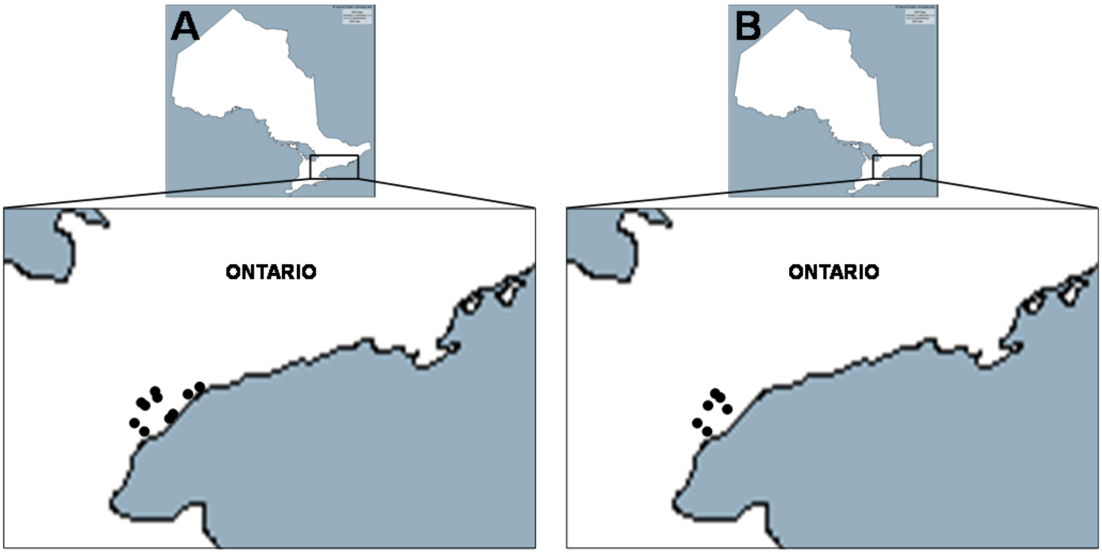
Abbreviations are as follows: **Invasive tree** *A.*: Acacia, *Ac.*: Acer, *Ad.*: Adenanthera, *Ai.*: Ailanthus, *Al.*: Alstonia, *B.*: Bischofia, *C.*: Cinnamomum, *E.*: Elaeagnus, *Er.*: Eriobotrya, *Eu.*: Eugenia, *G.*: Gleditsia, *H.*: Homalanthus, *L.*: Ligustrum, *M.*: Melaleuca, *P.*: Paraserianthes, *Pa.*: Paulownia, *Pi.*: Pinus, *Pit.*: Pittosporum, *Pop.*: Populus, *Pr.*: Prosopis, *Pn.*: Prunus, *Ps.*: Pseudotsuga, *Pd.*: Psidium, *Q.*: Quercus, *R.*: Rhamnus, *Ro.*: Robinia, *S.*: Sandoricum, *Sa.*: Sapium, *Sc.*: Schinus, *So.*: Solanum, *Sy.*: Syzygum, *T.*: Tabebuia, *Ta.*: Tamarix, *U.*: Ulmus **Growth form (GrF)** BE: broadleaved evergreen, BD: broadleaved deciduous, C: conifer **Climate (Clim.)** A: arid, T: temperate, Tr: tropical, STr: 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 (InvHab)** C: coastal prairies, D: disturbed areas, F: forest, G: grasslands, O: open fields, R: riparian habitats, S: sand dunes, Sh: shrublands.

Appendix 15. List of the source populations of *Acer negundo* and *Acer platanoides*.

Range	Continent	State/ Country	Collection site	Latitude/ Longitude
Acer negundo				
Native	North America	Ontario	Don Valley East 1	43°46' N, 79°21' W
	North America	Ontario	Don Valley East 2	43°48' N, 79°22' W
	North America	Ontario	Don Valley West 1	43°45' N, 79°26' W
	North America	Ontario	Don Valley West 2	43°45' N, 79°25' W
	North America	Ontario	Glen Rouge	43°48' N, 79°08' W
	North America	Ontario	Humber River	43°39' N, 79°30' W
	North America	Ontario	King's Mill	43°38' N, 79°29' W
	North America	Ontario	Morningside park	43°46' N, 79°11' W
	North America	Ontario	Taylor Creek 1	43°42' N, 79°18' W
	North America	Ontario	Taylor Creek 2	43°42' N, 79°19' W
Invasive	Europe	France	Rivière	43°40' N, 01°08' W
	Europe	France	Saubusse	43°39' N, 01°11' W
	Europe	France	Pontonx-sur-l'Adour	43°47' N, 00°55' W
	Europe	France	Cestas	44°45' N, 00°40' W
	Europe	France	Bruges	44°54' N, 00°36' W
	Europe	France	Moulon-port	44°51' N, 00°13' W
	Europe	France	Castillon-la-Bataille	44°51' N, 00°02' W
	Europe	France	St-Denis-de-Pile	44°59' N, 00°12' W
	Europe	France	Sablons	45°19' N, 04°45' E
	Europe	France	Condrieu	45°27' N, 04°47' E
Acer platanoides				
Native	Europe	France	Gradignan - Talence	44°45' N, 00°36' W
	Europe	France	Blanquefort	44°54' N, 00°38' W
	Europe	France	Montpezat	44°20' N, 00°31' E
	Europe	France	Buzet-sur-Baïse	44°15' N, 00°18' E
	Europe	France	Ambax	43°21' N, 00°56' E
	Europe	France	St Lary-Boujean	43°13' N, 00°44' E
	Europe	France	Lacq-Audéjos	43°24' N, 00°37' W
	Europe	France	Barèges	42°53' N, 00°03' E
	Europe	France	Gez - Cauterets	42°53' N, 00°06' W
	Europe	France	Grenoble	45°11' N, 05°43' E
Invasive	North America	Ontario	Brickworks park	43°40' N, 79°22' W
	North America	Ontario	Don Valley East	43°47' N, 79°22' W
	North America	Ontario	Don Valley West	43°45' N, 79°26' W
	North America	Ontario	Humber River	43°39' N, 79°30' W
	North America	Ontario	King's Mill	43°38' N, 79°29' W
	North America	Ontario	Serena Gundy	43°43' N, 79°21' W



Appendix 16. Populations of *Acer negundo* (A) and *Acer platanoides* (B) sampled in Aquitaine, Midi-Pyrénées and Rhône-Alpes, France for the common garden experiment.

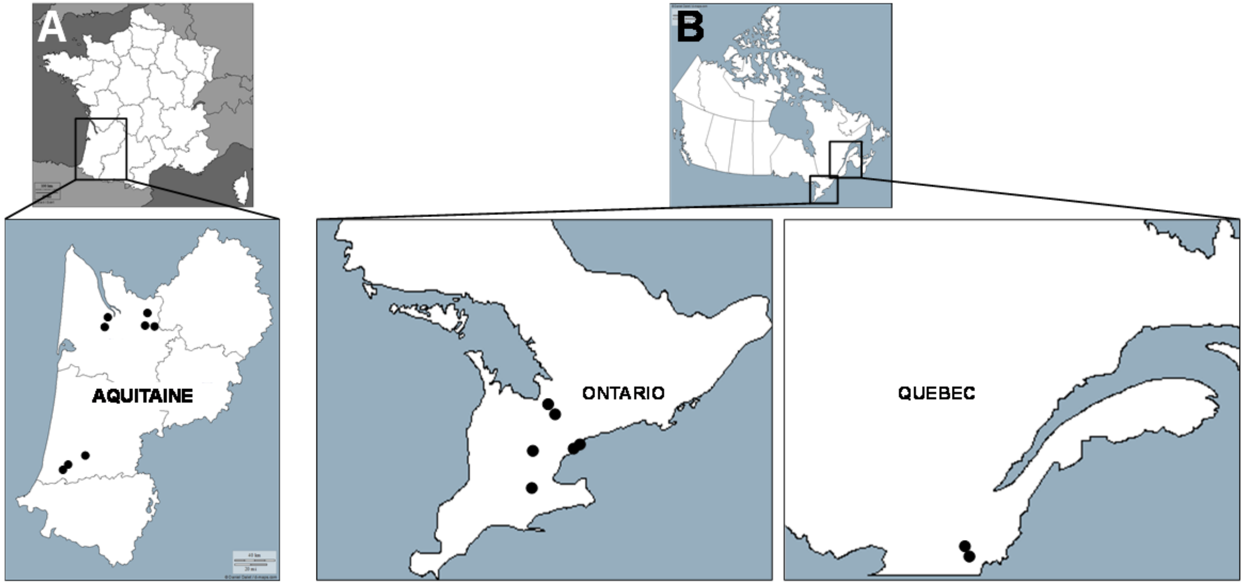


Appendix 17. Populations of *Acer negundo* (A) and *Acer platanoides* (B) sampled in southern Ontario, Canada for the common garden experiment.

Appendix 18. Means ± SE of life-history traits (survival, growth, phenology, physiology and leaf morphology) of native and invasive populations of *Acer negundo* and *Acer platanoides* grown in two reciprocal common gardens.

	Acer negundo				*Acer platanoides*			
	Canada		France		Canada		France	
Traits	Invasive	Native	Invasive	Native	Invasive	Native	Invasive	Native
Survival	0.73	0.96	0.63	0.74	0.51	0.56	0.70	0.71
Diameter	8.31 ± 0.10	8.36 ± 0.10	15.88 ± 0.50	12.78 ± 0.36	6.17 ± 0.15	6.22 ± 0.13	10.21 ± 0.37	10.29 ± 0.28
Height	43.53 ± 3.26	51.06 ± 1.10	79.35 ± 2.91	72.13 ± 2.50	16.61 ± 2.91	16.36 ± 1.93	44.05 ± 2.96	50.02 ± 2.58
LU 2009	125.62 ± 0.21	118.75 ± 0.24	86.51 ± 0.33	84.42 ± 0.33	125.76 ± 0.40	125.76 ± 0.34	89.98 ± 0.47	89.52 ± 0.40
LU 2010	118.00 ± 0.39	108.90 ± 0.29	88.72 ± 0.32	93.49 ± 0.28	120.51 ± 0.39	120.55 ± 0.37	102.47 ± 0.35	102.51 ± 0.34
A_{area}	4.19 ± 0.25	5.35 ± 0.34	7.16 ± 0.32	8.82 ± 0.31	6.15 ± 0.33	5.25 ± 0.25	6.97 ± 0.26	6.50 ± 0.26
$\mathrm{N}_{\mathrm{area}}$	0.90 ± 0.04	1.43 ± 0.06	1.24 ± 0.02	1.69 ± 0.05	0.94 ± 0.04	0.92 ± 0.04	1.65 ± 0.04	1.77 ± 0.05
PNUE	5.05 ± 0.44	4.06 ± 0.27	5.87 ± 0.24	5.44 ± 0.26	7.18 ± 0.56	5.91 ± 0.30	4.37 ± 0.19	3.79 ± 0.19
LMA	53.15 ± 1.72	70.19 ± 2.12	41.07 ± 0.85	52.68 ± 1.21	57.90 ± 0.95	61.18 ± 1.27	67.72 ± 1.05	72.03 ± 1.40

Notes: Terms are defined as follow: Survival, proportion; Diameter, mm; Height, cm; LU 2009: leaf unfolding in 2009, day of the year; LU 2010: leaf unfolding in 2010, day of the year; A_{area}: maximum assimilation rate per leaf area, µmol $\mathrm{CO_2.m^{-2}.s^{-1}}$; $\mathrm{N}_{\mathrm{area}}$: leaf N content per leaf area, $\mathrm{gN.m^{-2}}$; PNUE: photosynthetic N-use efficiency, µmol $\mathrm{CO_2.g^{-1}N.s^{-1}}$; LMA: leaf mass per area index, $\mathrm{g.m^{-2}}$.



Appendix 19. Populations of *Acer negundo* sampled in Aquitaine, France (A; introduced range) and Ontario and Québec, Canada (B; native range) to examine intraspecific differences in phenotypic plasticity to nutrient availability.

Appendix 20. Means ± SE for traits related to growth, gas exchange and leaf morphology, biomass and biomass allocation of eight native and eight invasive populations of *Acer negundo* growing along a nutrient gradient. Sample sizes are $n = 24$ for growth traits, $n = 4$ for physiology traits and $n = 6$ for leaf morphology and biomass related traits. See text for definition of terms.

Traits	Low nutrient level		Medium nutrient level		High nutrient level	
	Invasive	Native	Invasive	Native	Invasive	Native
Growth						
Height	104.15 ± 2.24	92.51 ± 2.37	133.03 ± 2.55	111.58 ± 2.87	138.08 ± 2.89	112.45 ± 2.67
Diameter	9.69 ± 0.16	10.34 ± 0.16	11.35 ± 0.17	11.86 ± 0.18	12.06 ± 0.23	12.81 ± 2.22
Leaf traits						
A_{area}	2.90 ± 0.17	3.00 ± 0.24	5.30 ± 0.33	5.38 ± 0.35	6.48 ± 0.44	6.53 ± 0.41
A_{mass}	0.11 ± 0.01	0.11 ± 0.01	0.18 ± 0.01	0.18 ± 0.02	0.21 ± 0.01	0.20 ± 0.01
$\mathrm{N}_{\mathrm{area}}$	0.38 ± 0.01	0.47 ± 0.02	0.62 ± 0.03	0.73 ± 0.03	1.10 ± 0.04	1.32 ± 0.06
$\mathrm{N}_{\mathrm{mass}}$	1.42 ± 0.07	1.57 ± 0.09	2.08 ± 0.08	2.34 ± 0.11	3.64 ± 0.07	3.87 ± 0.06
PNUE	7.64 ± 0.55	6.61 ± 0.54	9.10 ± 0.53	8.18 ± 0.70	5.83 ± 0.30	5.07 ± 0.27
LMA	28.62 ± 0.98	32.24 ± 1.35	30.63 ± 1.07	33.41 ± 1.40	30.28 ± 1.13	34.23 ± 1.38
L_{s}	34.32 ± 2.03	44.55 ± 2.45	39.02 ± 1.48	49.09 ± 2.58	47.92 ± 1.95	54.61 ± 2.23
Biomass						
W_{l}	4.31 ± 0.46	3.96 ± 0.34	7.27 ± 0.48	7.35 ± 0.52	9.21 ± 0.74	8.90 ± 0.60
W_{s}	19.48 ± 2.05	15.34 ± 1.39	28.54 ± 2.09	25.89 ± 1.93	30.63 ± 2.91	29.86 ± 2.18
W_{r}	7.78 ± 0.81	10.29 ± 0.75	11.17 ± 1.04	14.41 ± 1.19	10.76 ± 1.08	14.63 ± 1.04
W_{t}	31.58 ± 3.22	29.71 ± 2.43	47.45 ± 3.41	47.43 ± 3.44	50.61 ± 4.62	53.39 ± 3.71
W_{a}	23.80 ± 2.47	19.30 ± 1.68	35.81 ± 2.53	33.24 ± 2.39	39.85 ± 3.59	38.76 ± 2.74
A_{l}	0.144 ± 0.015	0.128 ± 0.012	0.240 ± 0.015	0.217 ± 0.014	0.292 ± 0.021	0.253 ± 0.016
Biomass allocation						
RSR	0.370 ± 0.022	0.580 ± 0.022	0.306 ± 0.017	0.455 ± 0.022	0.269 ± 0.010	0.401 ± 0.016
LWR	0.137 ± 0.005	0.134 ± 0.006	0.169 ± 0.006	0.162 ± 0.006	0.197 ± 0.007	0.174 ± 0.005
SWR	0.600 ± 0.010	0.504 ± 0.010	0.602 ± 0.008	0.532 ± 0.010	0.594 ± 0.006	0.544 ± 0.008
RWR	0.262 ± 0.010	0.362 ± 0.009	0.228 ± 0.010	0.305 ± 0.011	0.210 ± 0.006	0.282 ± 0.007
LAR	0.0051 ± 0.0003	0.0046 ± 0.0003	0.0061 ± 0.0005	0.0055 ± 0.0004	0.0072 ± 0.0004	0.0057 ± 0.0004

Appendix 21. Intraspecific comparisons of phenotypic plasticity in invasive plants. Summary of studies comparing phenotypic plasticity between native and invasive populations of exotic plant species in response to variation in environmental conditions. Plasticity was reported for various traits related to biomass (B), defense to herbivory (D), growth (G), leaf morphology (M), phenology (Pe), physiology (P) and reproduction (R).

Invasive species	Functional group	Abiotic factors	Traits	Plasticity	Conclusion	References
Alliaria petiolata	Biennial forb	Nutrient, water	G, P	Inv = Nat	No post-introduction evolution	[1]
Centaurea stoebe	Perennial forb	Nutrient, water, site	G, M, P, R	Inv = Nat	Pre-adaptation	[2]
Ceratophyllum demersum	Perennial forb (aquatic)	Temperature	G, M, P	Inv > Nat	Post-introduction evolution	[3,4]
Clidemia hirta	Perennial shrub	Light	B, G, P	Inv = Nat	No genetic shift	[5]
Cynoglossum officinale	Biennial forb	Site	G, R	Inv > Nat	Founder effects	[6]
		Nutrient	G, R	Inv = Nat	Founder effects	
Eupatorium adenophorum	Perennial forb	CO_2	B, G	Inv = Nat	-	[7]
Hypericum perforatum	Perennial forb	Site	D	Inv = Nat	-	[8]
Lythrum salicaria	Perennial forb	Nutrient	B, R	Inv > Nat	-	[9]
		Nutrient, water	B, G	Inv > Nat	Post-introduction evolution	[10]
Melaleuca quinquenervia	Tree	pH	G	Inv > Nat	-	[11]
Microstegium vimineum	Annual grass	Light, site	B, G, M	Inv = Nat	-	[12,13]
Mimulus guttatus	Annual forb	Water	G, Pe, R	Inv = Nat	No selection	[14]
Phalaris arundinacea	Perennial grass	Soil moisture	G, M	Inv > Nat	Post-introduction evolution	[15]
Plantago lanceolata	Perennial forb	Temperature	R	Inv = Nat	-	[16]
Senecio inaequidens	Perennial shrub	Nutrient	B	Inv > Nat	Post-introduction evolution	[17]
Senecio pterophorus	Perennial shrub	Disturbance, water	B, M, R	Inv > Nat	Selection	[18]
Spartina alterniflora	Perennial grass	Nutrient	B, G, M	Inv > Nat	Post-introduction evolution	[19]
		Nutrient	P	Inv = Nat	-	
Taraxacum officinale	Perennial forb	Water	B, M, P	Inv < Nat	Local adaptation	[20]
		Water	B	Inv < Nat	-	[21]
		Nutrient	B	Inv = Nat	-	
Triadica sebifera	Tree	Light	B, M	Inv > Nat	Post-introduction evolution	[22]
		Water	B	Inv = Nat	Pre-adaptation	

Inv: invasive populations, Nat: native populations, Inv = Nat: no difference in plasticity between native and invasive populations, Inv > Nat: invasive populations have greater phenotypic plasticity than native populations, Inv < Nat: invasive populations have lower phenotypic plasticity than native populations. Site factor is the effect of common gardens.

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