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Research

Biogeographical contrasts to assess local and regional patterns of invasion: a case study with two reciprocally introduced exotic maple trees

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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.

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 alters 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 (Manitoba maple), native to northeastern America has been introduced intentionally into many regions throughout Europe since 1688 for horticultural purposes (Medrzycki 2007). It often occurs in dense monospecific stands and grows in disturbed sites, along roadsides, in abandoned fields, and is very widely distributed throughout Europe now (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 disturbances such as floods and high soil nutrient levels (Tabacchi and Planty-Tabacchi 2003).

Acer platanoides (Norway maple), native to Europe, has become a commonly planted street tree in North America since its intentional importation as a shade tree to Philadelphia in the mid-to-late 1700s (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 rapidly spread into urban woodlands (Bertin et al. 2005) as well as intact forests particularly in the northeastern United States (Webb and Kaunzinger 1993), wherein it has been shown to reduce understorey biodiversity (Wyckoff and Webb 1996). This species is now 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 (Supplementary material Appendix 1, Table A1, A2). 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 (Supplementary material Appendix 1, Table A3). The sampled forests were chosen when they met the three following criteria: 1) being within the defined region area, 2) specifically matching the type of habitat usually invaded by the target maple tree species, and 3) 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 × 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, $\chi^2 = 4.3387$, $p = 0.1183$, DF = 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, $\chi^2 = 25.9442$, $p < 0.0001$, DF = 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, $r^2 = 0.91$, $p = 0.0008$, DF = 6, Fig. 3) but no effect of the introduced *A. platanoides* populations on native tree species in Canada (linear regression, $r^2 = 0.09$, $p = 0.38$, DF = 9, Fig. 3). Importantly, there were no significant effects of either maple species on other native species in their respective home ranges (linear regressions, $r^2_{A.\ negundo} = 0.03$, $p = 0.55$, DF = 1; $r^2_{A.\ platanoides} = 0.02$, $p = 0.78$, DF = 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, $\chi^2 = 13.6969$, $p = 0.0011$, DF = 2). In southern France, most of the riparian corridors surveyed at the regional scale were invaded by *A. negundo* (Fig. 4). The species formed monospecific stands along Adour and Dordogne Rivers, whilst the downstream on the Garonne River only was uninvaded (Supplementary

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	DF	χ^2	p-value	Post hoc
Density				
Species	1	9.5406	**0.0020**	AN > AP
Range	1	9.9898	**0.0016**	Inv > nat
Species × range	1	7.3552	**0.0067**	Inv (AN) > nat (AN), inv (AP), nat (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**	Inv > Nat
Species × range	1	13.9469	**0.0002**	Inv (AN) > nat (AN), inv (AP), nat (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.

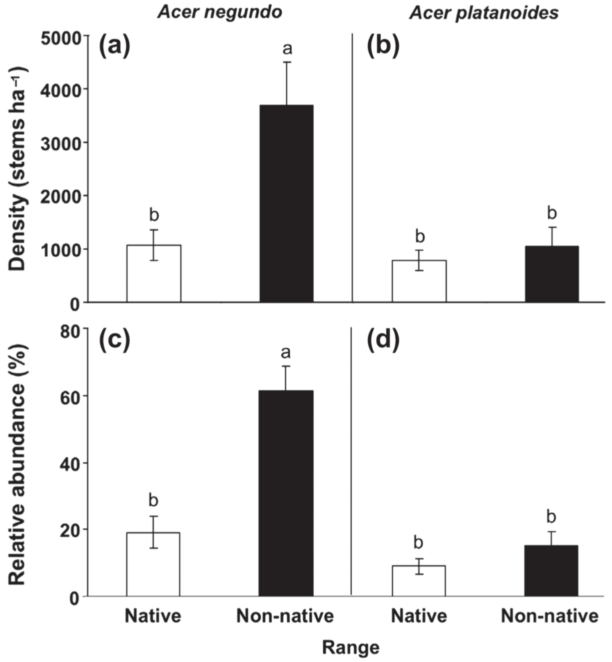

Figure 1. The density and relative abundance of *Acer negundo* (a, c) and *Acer platanoides* (b, d) populations in their native and non-native ranges. Bars show means ± SE of populations from southern Ontario, Canada (n = 20) and southern France (n = 14). $^{***}p < 0.001$, $^{**}p < 0.01$.

material Appendix 1, Table A3). 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.

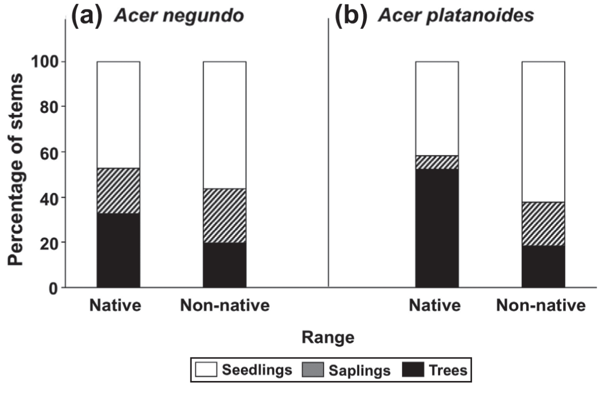

Figure 2. The age structure of *Acer negundo* (a) and *Acer platanoides* (b) populations in their native and non-native ranges.

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

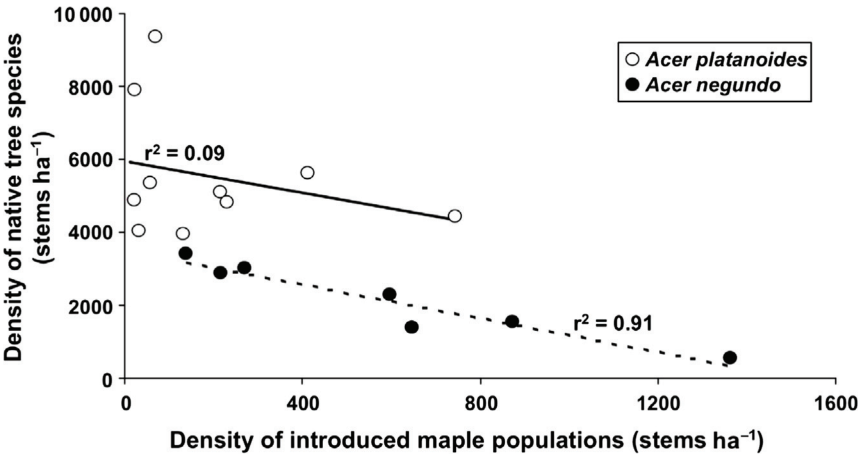

Figure 3. The relationship between the density of *Acer negundo* and *Acer platanoides* and native tree species of the recipient communities. In southern France (*Acer negundo* non-native range), n = 7, and n = 10 in southern Ontario, Canada (*Acer platanoides* non-native range).

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

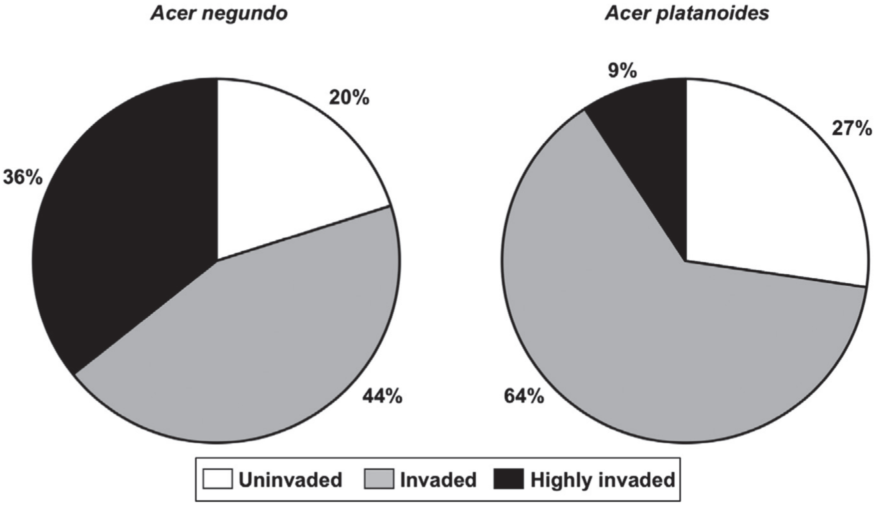

Figure 4. The regional distribution of *Acer negundo* populations in southern France and *Acer platanoides* populations in southern Ontario, Canada. Forests sampled in the non-native range of both species were classified as uninvaded (species absent), invaded (species present with up to 5 individuals, 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.

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 differ 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 highlights 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 Säumel 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 (Säumel 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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Supplementary material (Appendix E7300 at < www.oikosoffice.lu.se/appendix >). Appendix 1.