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Parent tree distance-dependent recruitment limitation of native and exotic invasive seedlings in urban forests

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Abstract Urban forests are more vulnerable to exotic species invasions than natural forests and are often a pathway for exotic invasions into natural areas. Investigating the mechanisms responsible for species coexistence in urban ecosystems is important to prevent forest invasions and conserve native biodiversity. In this experiment, we studied seedling recruitment for two exotic invasive (*Acer platanoides* and *Rhamnus cathartica*) and two native tree species (*Acer saccharum* and *Betula papyrifera*) in two urban forests. We measured the effects of distance from a mature tree on the growth of conspecific seedlings and their belowground interactions (mutualisms and pathogens). We expected that native seedlings growing in close proximity to a mature conspecific tree would more likely be damaged by co-specific pathogens than those growing further away. In contrast, considering that exotic invaders have not coevolved with the local soil pathogens, distance from the adult conspecific tree would not affect their seedlings. We collected undisturbed soil cores at five incremental distances from each adult tree and grew conspecific seeds in these cores. After three months of growth, we measured plant biomass, mycorrhizal root colonization and root lesions. We found that biomass increased with distance from the mature conspecific tree only for *A. platanoides* and no distance dependent signal was detected for other response variables. Our results show that distance from a conspecific mature tree may not determine exotic species invasibility in an urban forest and that, instead, this may contribute to promote native and invasive species coexistence in urban forest systems.

Keywords Invaded ecosystems · Janzen Connell hypothesis · Mycorrhizal fungi · Recruitment limitation · Species coexistence · Urban forests

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Introduction

Exotic plant species invasion is a major threat to global biodiversity and natural ecosystems. As such, explaining exotic plant invasion mechanisms has been a central question over the last two decades (Kueffer et al. 2013; Mack and Rudgers 2008; Simberloff et al. 2013). Investigating the mechanisms of native and exotic plant species coexistence is necessary to better understand and predict the dynamics of invasions. Many plant invasions tend to form monospecific stands which require high seedling recruitment (i.e., high proportion of new individuals able to germinate and grow in the foreign environment). In natural forest ecosystems, native species coexistence is maintained by native seedling recruitment limitation assuming that host specific parasites (e.g., pathogens and herbivores) are more likely to damage conspecific seeds and seedlings the closer they germinate to the parent tree (distance-dependent coexistence mechanism explained by the Janzen and Connell Hypothesis (Connell 1971; Janzen 1970)). Biogeographic studies have supported the parent tree distance-dependent mechanism to explain species coexistence across latitudinal gradients from boreal to temperate systems and across different ecological guilds (Comita et al. 2014). However, it is still unknown if distance-dependent mechanisms in regard to recruitment limitation apply to closed-canopy urban forest ecosystems invaded by exotic invasive plant species (hereafter invasive species). Invasive species spread rapidly in their introduced range because they may have escaped from their co-evolved specific pathogens (Enemy Release hypothesis; Keane and Crawley 2002) and may have acquired better belowground mutualisms (Enhance Mutualisms hypothesis; Reinhart and Callaway 2006). Therefore, if invasive species leave their specific enemies behind, a disruption to distance-dependent mechanisms can be expected in invaded ecosystems leading to shifts in plant community structure, including the denser populations of invasive species where seedling recruitment is not dependent on the distance from the parent tree.

Soil biotic communities are important regulators of plant community structure determining plant species abundance and invasiveness by dynamic feedbacks (Klironomos 2002). The net effect of pathogenic and mutualistic interactions controls the direction and the strength of plant-soil feedbacks (Bever 2003). In natural forest ecosystems, negative feedbacks increase with proximity to conspecific adult trees due to the detrimental impact of specialist soil pathogens on plant performance (Bever et al. 2010). Conversely, in invaded ecosystems, the potential absence of host-specific soil pathogens of exotic invasive plant species may attenuate negative feedbacks resulting in dense monoculture patches. In fact, previous studies have shown that nearest conspecific neighbour distance between exotic trees in invaded ecosystems is smaller than in their native ranges (Reinhart and Callaway 2004; Reinhart et al. 2003). Additionally, associations between exotic plant species and soil mutualisms can lead to positive feedbacks, which enhance exotic species abundance (Callaway et al. 2004). Despite many studies focusing on the mechanisms underlying invasive species success, little work has examined mechanisms associated to the co-existence of native and invasive species in forests (Martin and Canham 2010). Understanding the mechanisms underlying invasive species establishment and population dynamics is important to anticipate the long-term consequences of invasions on both the biodiversity and spatiotemporal dynamics of forest ecosystems.

Since exotic species introductions occur primarily in urban forests, these are also excellent systems to explore the mechanisms that may facilitate invasive species establishment (González-Moreno et al. 2013; Mandryk and Wein 2006) and from there, predict forest ecosystem dynamics in the context of disturbance. Even though undisturbed forests are thought to be more resistant to invasive plant species (Sanderson et al. 2012; Von Holle et al. 2003), evidence of forest invasion by plants initially introduced for landscape purposes is high (Martin et al. 2008). Urban forests are usually highly invaded (Vilà and Ibáñez 2011), representing a pathway to exotic invasions of natural (i.e. less disturbed) forests. Accordingly, further insights into the ecological mechanisms underlying urban biological invasions are necessary to develop appropriate policies and management practices for urban ecosystems.

In this study we tested the conspecific tree distance effect on the seedling growth and the belowground interactions of two native and two invasive exotic species coexisting in mixed deciduous urban forests. We measured plant growth and net effects of belowground mutualistic and antagonistic interactions to assess the effect of distance from conspecific adult trees on recruitment limitation. We used mycorrhizal symbioses as a model to investigate the mutualistic effect. Antagonistic interactions were evaluated by quantifying the incidence of root lesions. Hypothetically, since pathogen build up should result in less carbon available for symbioses, higher root mycorrhizal colonization to lesions ratio may indicate a greater effect of mutualistic interactions and vice versa. We hypothesized that distance-dependent effects on conspecific seedlings are present for the native species in urban forests but not for invasive species since exotic invaders may have escaped from their co-evolved specific pathogens and may potentially have acquired even better belowground mutualisms than those in their native range. More specifically, we tested the following hypotheses:

> H1 – Seedling growth of native plant species increases with distance from conspecific adult trees. However, this does not apply to exotic invasive plant species;
> H2 – Root mycorrhizal colonization : lesions ratio increases with distance from native conspecific trees but remains unchanged for exotic invasive plant species.

Methods

Site and experimental conditions

The study was conducted in two highly invaded forest stands located in the city of Sault Ste. Marie (Stand 1: 46° 31’ 6.09” N/84° 18’ 0.32” W, and Stand 2: 46° 30’ 33.45”N/84° 15’ 22.42” W: Ontario, Canada). In each forest stand, we selected pairs of the most abundant native and exotic invasive tree species in that stand. Target plants from the first stand were the native Sugar maple, *Acer saccharum* and the exotic invasive Norway maple, *Acer platanoides.* Target plants from the second stand were the native White birch, *Betula papyrifera* and the invasive Common buckthorn, *Rhamnus cathartica.* We selected six adult trees of similar trunk diameter for each target species in November 2013. Previous studies indicate that parent tree influence on seed dispersion and seedling survival are significant within the first five meters from a parent tree (Gomez-Aparicio et al. 2008; Martin and Canham 2010) and therefore, each of the target conspecific trees were at least 10 m apart from each other to minimize any potential non-independence among experimental units.

We conducted a greenhouse experiment to control for seed germination timing, soil moisture content and to avoid aboveground herbivory and other disturbances typical of urban forests. Five undisturbed soil cores (8 cm diameter by 20 cm deep PVC pipe) were collected across a two meter transect at 0 m, 0.3 m, 0.6 m, 1.2 m and 2 m from each conspecific tree and consistently following the same orientation. We did not cover a distance greater than two meters because it would have overlapped with the effect from neighboring conspecific trees. In addition, previous studies have shown distance dependent growth effects in the first 5 m from a conspecific tree (Gomez-Aparicio et al. 2008; Martin and Canham 2010; Schupp and Frost 1989). Forest litter was collected under the canopy of each species and dried at 50 °C for 4 days. A soil sample from each soil core location was collected to characterize soil chemical properties. Soil cores were kept at 4 °C until the onset of the greenhouse experiment.

Soil water content was calculated by weighting a 2 mm sieved soil sample before and after freeze-drying. Carbon (C) and nitrogen (N) soil content was measured to determine whether or not soil fertility varied within the 2 m transect. This was conducted using a C, N analyzer (Flash 2000 CHNS/O Analyzers, Thermo Scientific, Cambridge UK).

Seeds from *A. saccharum* and *B. papyrifera* were supplied by the National Tree Seed Center (Natural Resources Canada). *Acer platanoides* and *R. cathartica* seeds were collected from naturalized trees in Sault Ste. Marie's urban forests since it was assumed this species would be easier to germinate and seeds are not commercially available. *Acer* seeds were separated from the samara and *R. cathartica* seeds were thoroughly washed to remove the fleshy fruit. All seeds were immersed in deionized water for 2 days. The seeds were then surface sterilized with hydrogen peroxide (15 %) for 40 min and rinsed with autoclaved deionized water. The processed seeds were cold stratified by incubation in sterilized wet media (1:1 peat moss/sand) at 4 °C for 61 days to mitigate the dormancy.

The greenhouse experiment started in January 2014. Lights were set up at 600 ftc in 16:8 h day : night cycles. Mean greenhouse temperature increased from 7 °C to 18 °C during the experiment to reach ideal germination temperatures for the different species according to the "Silvics of North America" handbook (Burns and Honkala 1990). Each soil core received 6 seeds from the conspecific sampled tree and 1 g of litter from the sampled forest stand. Soil cores were randomized weekly. Mean soil water content of the soil cores from each forest stand was calculated and cores were weighted and watered weekly accordingly to maintain the same soil water content within species treatments. Cores were kept in saucers to avoid cross-contamination and potential nutrient loss through leaching. Germination was recorded twice a week. After 50 days of growth, the number of seedlings per core was reduced to one, thus avoiding plant-plant competition.

Harvest

Twelve weeks after germination, for each species treatment, tree seedlings were cut at the soil surface, dried at 55 °C for 4 days and weighted. Previous experiments have shown seedling biomass reductions caused by pathogens in under 12 weeks of growth (i.e., 10 weeks in Packer and Clay 2003). Roots were washed with tap water to remove soil particles. Lateral roots were taken from the entire root system from each plant and cut into small pieces (ca. 1 cm). Ectomycorrhizal roots from *B. papyrifera* were placed in a Petri dish containing water. The percentage of mycorrhizal short roots for each *B. papyrifera* seedlings was assessed by counting at least 200 short roots using a stereomicroscope (Parladé et al. 1996).

Following Phillips and Hayman (1970), roots of arbuscular mycorrhizal (AM) fungal species (i.e., *A. saccharum*, *A. platanoides* and *R. cathartica*) were stained with trypan blue. Total AM fungal colonization was assessed using the gridline intersection method by McGonigle et al. (1990). For each sample, at least 100 line intersections were examined and the presence of hyphae, vesicles, and arbuscules was scored.

The incidence of root enemy attack was estimated by visually quantifying root lesions (Fig. 1). Since a standard protocol for this technique is not available in the literature, lesions were recorded as injuries and root decay. An injury consisted of a discrete area of darker adjacent cells, or missing groups of adjacent cells with the immediate surrounding intracellular space darkened or intact (Fig. 1b, c). Rood decay consisted of the darkening of a single or more cells (Fig. 1c). This approach provides a consistent estimate of plant tolerance against pathogens and other enemies (Mitchell 2003). Although visual disease estimates may underestimate disease effects on plant growth, it provides a consistent estimate of primarily fungal damage among treatments (Schnitzer et al. 2010). The mutualistic and antagonistic net effect by mycorrhizal fungi and soil borne pathogens was estimated by calculating the mycorrhizal root colonization to root lesions ratio (mycorrhizal : lesions). Higher mycorrhizal: lesions ratio indicates higher incidence of mutualistic interactions and, conversely, lower mycorrhizal : lesions ratio indicates larger pathogenic effects.

Statistics

Statistical analysis and graphs were performed using R (R Development Core Team 2013). Correlation between C and N was tested using function 'lm' from R *stats* package. Linear mixed-effects models were used to test the impact of distance on C content for each plant species. The 'lmer' function from *lme4* R package (Bates et al. 2014) was used setting distance as a fixed factor and tree transect as a random effect.

Above, below and total biomass were analyzed using linear mixed effects models with distance, C, and growing days as fixed factors and tree transect as a random effect. Individual models were fit for each tree species using function 'lmer' from *lme4* R package (Bates et al. 2014). The best fitting model was simplified by stepwise removal of co-variables, using maximum likelihood methods to compare models and choosing the model with lowest AIC (Crawley 2012).

Significance of total ectomycorrhizal colonization, AM fungal hyphal, arbuscular and vesicular colonization and root lesions were determined fitting generalized linear mixed effect model using the 'glmer' function (family set to binomial). When the data were over-dispersed (tested with the function 'overdisp_fun'; http://glmm.wdfiles.com/local–files/trondheim/glmm_funs.R) and an individual –level random effect was added to the equation model (Breslow 1990). Stepwise simplification process was used to choose the best fitting model.

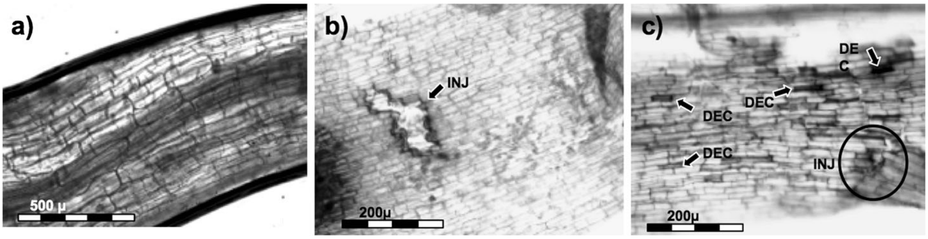

Fig. 1 **a** Root without lesions (*Betula papyrifera*), **b** Injury (*Rhamnus cathartica*), **c** Root decay and injury (*Rhamnus cathartica*). DEC: Decay, INJ: Injury

Results

Soil C and N content were highly correlated ($R^2 = 93.8$ %, $P < 0.001$) and did not significantly change with distance from the tree for any of the target plant species (Table 1).

Acer platanoides seeds started germinating 15 days after planting when the mean temperature was 7 °C whereas seeds of *A. saccharum* germinated after 30 days, when the mean temperature was 10 °C. *Rhamnus cathartica* and *B. papyrifera* seeds started geminating after 2 months when the mean greenhouse temperature was 15 °C.

Distance dependent effects on shoot, root and total biomass were significant for *A. platanoides* (biomass increased with distance from the tree) (Fig. 2). However, distance from conspecific adult tree did not have a significant effect on the biomass of the other three species (Table 1, Fig. 2). Stepwise model simplification indicated that different numbers of growing days between seedlings did not influence biomass, however, soil C content had a negative effect on *B. papyrifera* biomass (Table 2).

Total arbuscular mycorrhizal colonization of *A. platanoides*, *A. saccharum* and *R. cathartica* was 63 % ± 4.0, 61.5 % ± 4.6 and 61.19 % ± 2.4 (mean and standard error) respectively (Table 3). *Acer saccharum* had the lowest arbuscular colonization (18.39 % ± 3.0), followed by *A. platanoides* (28.74 % ± 3.0), and by *R. cathartica* (61.19 % ± 2.4) (Table 3). Mean percentage of ectomycorrhizal colonization of *B. papyrifera* was 36.6 % ± 5.7 (Table 3).

Distance from conspecific adult tree did not influence total ecto- or endomycorrhizal colonization. However, vesicle abundance in *A. saccharum* roots increased with distance from the conspecific adult tree (Table 4). Opposite effects were found for vesicular colonization of *R. cathartica* roots (Table 4). Differences in growing days did not have a significant effect on mycorrhizal variables, however, soil C content positively influenced the amount of *A. saccharum* arbuscular colonization and ectomycorrhizal colonization of *B. papyrifera*.

Rhamnus cathartica was more affected by root lesions than *A. platanoides*, *A. saccharum* and *B. papyrifera* (Table 3). However, distance from the conspecific adult tree did not influence the amount of root lesions for any of the tested plant species (Table 4). The mycorrhiza : lesions ratio did not respond to distance for any of the tested plant species, yet the model showed that soil C content had a significant effect on *B. papyrifera* mycorrhiza : lesions ratio.

Discussion

Our study investigates mechanisms of coexistence between native and exotic invasive tree species in deciduous urban forests within the Great Lakes – St. Lawrence Forest Region. It demonstrates that distance from a conspecific tree affected seedling recruitment of the tested

Table 1 F test and *p*-values for the linear mixed-effects model to test the effect of distance from the mature tree on C soil content. Mean and standard errors of soil nitrogen (N), carbon (C) and water content

Tree Species	$F_{(1,\ 30)}$	*P* - value	Soil N (%)	Soil C (%)	Soil Water Content (ml)
Acer platanoides	<0.0001	0.99	0.19 ± 0.01	2.61 ± 0.18	30.58 ± 0.86
Acer saccharum	0.18	0.67	0.24 ± 0.01	3.09 ± 0.13	29.32 ± 1.25
Rhamnus cathartica	0.03	0.86	0.36 ± 0.02	5.17 ± 0.24	44.02 ± 1.44
Betula papyrifera	0.07	0.79	0.37 ± 0.02	5.55 ± 0.28	42.73 ± 1.50

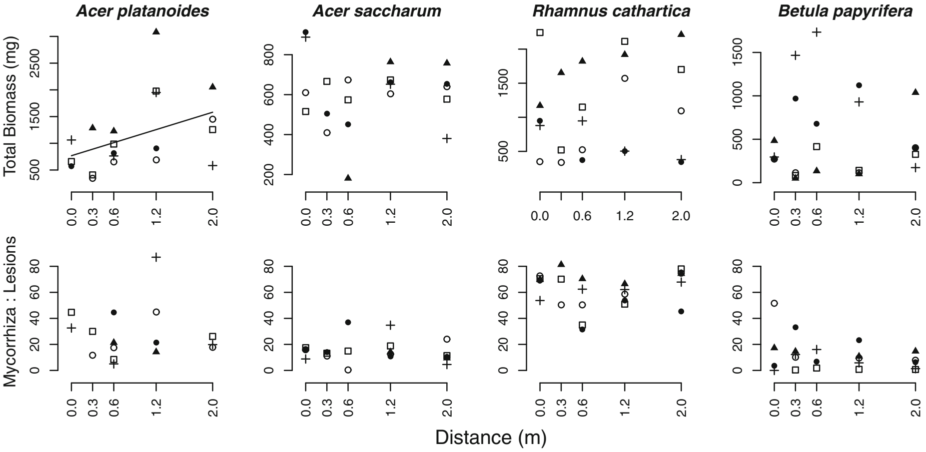

Fig. 2 Total biomass (mg) and root mycorrhizal : lesions ratio across 2 m perpendicular transects for *Acer platanoides*, *Acer saccharum*, *Rhamnus cathartica* and *Betula papyrifera*. *Solid line* indicates significant effect of distance according to the mixed effects model. Different symbols represent different replicated transects

species differently and not as hypothesised. We expected that conspecific distance-dependent effects on seedling growth (H1) and root mycorrhizal colonization : lesions ratio (H2) would be restricted to native species. Instead, from the four target species, only the biomass of invasive *A. platanoides* seedlings increased with distance from the conspecific adult tree and

Table 2 Parameter estimates, standard error, F test and *p*-values for the best fitted linear mixed effect models to measure the effect of distance from parent tree on shoot, root and total biomass of *Acer platanoides Acer saccharum*, *Rhamnus cathartica* and *Betula papyrifera*. The models used tree-transect as a random effect, and distance and carbon (C) as fixed effects

Species	Variable	Predictor	Estimate	Std. Error	F test	*P* - value
Acer platanoides	Shoot Biomass	**Distance**	**158.57**	**60.94**	**6.77**	**0.020**[a]
	Root Biomass	**Distance**	**249.34**	**125.78**	**3.93**	**0.065**[b]
	Total Biomass	**Distance**	**406.97**	**177.25**	**5.27**	**0.036**[a]
Acer saccharum	Shoot Biomass	Distance	−11.51	34.43	0.11	0.741
	Root Biomass	Distance	5.09	24.45	0.04	0.837
	Total Biomass	Distance	−6.42	48.73	0.02	0.896
Rhamnus cathartica	Shoot Biomass	Distance	−16.48	63.75	0.07	0.798
	Root Biomass	Distance	55.92	85.08	0.43	0.518
	Total Biomass	Distance	39.36	144.60	0.07	0.788
Betula papyrifera	Shoot Biomass	Distance	1.05	48.81	0.00	0.983
		C	**−82.81**	**36.00**	**5.29**	**0.031**[a]
	Root Biomass	Distance	−2.03	61.73	0.00	0.974
		C	**−156.62**	**41.43**	**14.29**	**0.001**[a]
	Total Biomass	Distance	−0.65	108.81	0.00	0.995
		C	**−238.17**	**76.24**	**9.76**	**0.005**[a]

Significant ($P < 0.05$) and marginally significant ($P < 0.07$) effects are shown in bold

[a] Indicates significant differences

[b] Indicates marginal differences

Table 3 Mean percentage of arbuscular mycorrhizal (AM) root colonization of *Acer platanoides*, *Acer saccharum*, *Rhamnus cathartica* and *Betula papyrifera* (mean ± standard error of the mean)

Root colonization	*Acer platanoides* (%)	*Acer saccharum* (%)	*Rhamnus cathartica* (%)	*Betula papyrifera* (%)
AM (hyphal)	63 ± 4.0	61.5 ± 4.6	61.19 ± 2.4	–
AM (arbuscular)	28.74 ± 3.0	18.39 ± 3.0	42.69 ± 2.1	–
AM (vesicular)	8.6 ± 1.68	10.53 ± 1.56	8.88 ± 1.72	–
Ectomycorrhizal fungi	–	–	–	36.63 ± 5.73
Lesions	2.80 ± 0.51	5.5 ± 0.98	13.0 ± 0.97	4.50 ± 0.80
Mycorrhiza:Lesions	41.78 ± 8.98	17.92 ± 3.57	6.24 ± 0.88	11.29 ± 2.55

the net effect of belowground interactions (i.e., mycorrhizal : lesions) did not vary with distance from any of the conspecific adult tree species. Recruitment limitation plays an important role in determining community diversity and structure (Clark et al. 1998; Siemann and Rogers 2006). The fact that invasive species did not have a clear advantage over native species on increasing seedling recruitment under their canopy as hypothesized, may contribute to promote the coexistence between native and invasive species in urban forests. This is consistent with the proposition that diverse plant communities with novel mixtures of species that include exotic and native species is often the long term outcome of invaded forest ecosystems rather than the development of monospecific stands (Lugo 2004).

Aboveground effects

Despite potential enemy release by invasive exotic species, which could cause neutral distance effects on seedlings growing next to conspecific trees, our results showed that the growth of *A. platanoides* seedlings positively correlated with increasing distance from conspecific adult trees. This suggests that either this species may not have escaped its natural enemies (see Jeschke et al. 2012), or novel environmental factors capable of maintaining distance dependency effects may arise in the introduced range. This result is consistent with previous studies from Martin and Canham (2010) and Gomez-Aparicio et al. (2008) which also tested the distance dependence hypothesis for *A. platanoides* in non-native soil. In our experiment, the increase in shoot biomass with distance cannot be associated to the effect of belowground mutualistic or pathogenic interactions, since presence of mycorrhizal fungi or root lesions did not change with distance from the mature conspecific tree (Table 4). However, Reinhart and Callaway (2004) found that soil microorganisms harmed *A. platanoides* seedlings under conspecific tree canopies. It is difficult to explain why distance dependent effects were not detected for *A. saccharum* in this experiment since *A. platanoides* and *A. saccharum* are co-existing congeners and could potentially share pathogens. Nevertheless, given the lack of distant dependent effects for *A. saccharum*, *B. papyrifera* and the invasive *R. cathartica* in our study, distance dependent effects may not generally be an important driver of species diversity in invaded urban forests.

The fact we found negative distance dependent processes between *A. platanoides* and conspecific seedlings does not necessarily imply a smaller invasive potential for this species. Other factors such as interspecific competitive interactions may determine invasion success and the subsequent successional forest canopy composition. Furthermore, superior growth of *A. platanoides* seedlings, which were twice as large than those of *A. saccharum* (11.36 g ± 15.30

Table 4 Parameter estimates, standard error, *z*- and *p*-values for the best fitted linear mixed effect models to measure the effect of distance on arbuscular mycorrhizal (AM) root colonization (hyphae, arbuscules and vesicles) for *Acer platanoides*, *Acer saccharum* and *Rhamnus cathartica*, ectomycorrhizal colonization for *Betula papyrifera* and root lesions. The models used tree-transect as a random effect, and distance and carbon (C) as fixed effects

Species	Variable	Factor	Estimate	Std. Error	*z*- value	*P*-value
Acer platanoides	AM colonization	Intercept	1.33	0.28	4.72	<0.001
		Distance	0.08	0.23	0.34	0.733
	Arbuscules colonization	Intercept	−0.30	0.30	−1.01	0.315
		Distance	0.17	0.26	0.67	0.505
	Vesicles colonization	Intercept	−1.87	0.46	−4.05	<0.001
		Distance	0.28	0.40	0.71	0.475
	Root lesions	Intercept	−3.70	0.30	−12.47	<0.001
		Distance	−0.04	0.25	−0.17	0.864
	Mycorrhiza : Lesions	Intercept	−3.16	0.33	−9.54	<0.001
		Distance	−0.17	0.28	−0.60	0.552
Acer saccharum	AM colonization	Intercept	0.46	0.45	1.03	0.305
		Distance	0.15	0.25	0.61	0.54
	Arbuscules colonization	Intercept	−4.78	1.52	−3.15	0.002
		Distance	0.32	0.52	0.61	0.544
		C	**0.59**	**0.24**	**2.44**	**0.015**
	Vesicles colonization	Intercept	−1.82	0.45	−4.07	<0.001
		Distance	**0.54**	**0.25**	**2.18**	**0.029**
	Root lesions	Intercept	−3.18	0.26	−12.39	<0.001
		Distance	0.20	0.21	0.93	0.352
	Mycorrhiza : Lesions	Intercept	−2.63	0.36	−7.22	<0.001
		Distance	0.08	0.30	0.27	0.79
Rhamnus cathartica	AM colonization	Intercept	0.45	0.17	2.67	0.008
		Distance	0.04	0.14	0.32	0.752
	Arbuscules colonization	Intercept	0.01	0.17	0.07	0.946
		Distance	0.12	0.12	0.99	0.324
	Vesicles colonization	Intercept	−2.16	0.00	−903.81	<0.001
		Distance	**−0.23**	**0.00**	**−96.24**	**<0.001**
	Root lesions	Intercept	−1.94	0.11	−16.94	<0.001
		Distance	−0.01	0.06	−0.12	0.907
	Mycorrhiza : Lesions	Intercept	−1.59	0.20	−8.10	<0.001
		Distance	−0.01	0.14	−0.09	0.926
Betula papyrifera	Ectomycorrhizal colonization	Intercept	−0.98	0.95	−1.03	0.303
		Distance	0.24	0.30	0.81	0.42
		C	**0.67**	**0.26**	**2.57**	**0.01**
	Root Lesions	Intercept	−2.60	0.40	−6.53	<0.001
		Distance	0.24	0.20	1.20	0.23
		C	**−0.32**	**0.13**	**−2.42**	**0.02**
	Mycorrhiza : Lesions	Intercept	−3.42	0.82	−4.17	0.00
		Distance	0.24	0.28	0.87	0.38
		C	**0.55**	**0.23**	**2.39**	**0.02**

Significant effects ($P < 0.05$) are shown in bold vs 6.07 g ± 0.36 *A. platanoides* and *A. saccharum*, respectively), might confer them greater competitive ability in reaching the canopy level (see also Gomez-Aparicio et al. 2008). Taken together our results suggest that *A. platanoides* invades by growing further away from mature conspecifics and seedlings arising from abundant seed banks can quickly grow in height to fill in available space (Webb et al. 2001).

Belowground effects

While attack to the roots by host specific enemies can lead to seedling escape from adult conspecifics, common mycorrhizal networks between conspecifics may contribute to counteract this effect due to enhanced pathogen protection (Hood et al. 2004). However, we did not observe a distance dependent effect either on total mycorrhizal colonization or root lesions. The methodologies used to assess both types of mycorrhizal fungi and lesions in roots are robust (see Maron et al. 2014; Maron et al. 2011; Schnitzer et al. 2010). Therefore, the overarching conclusion of our study is that the impact of invasive plant species and other urban associated disturbances on soil nutrient cycling and other ecosystem level properties might mitigate or even cancel native plant-soil feedback dynamics associated with the conspecific tree distance–dependent hypothesis (Fricke et al. 2014; Petermann et al. 2008). Additionally, the high invasive pressure of the studied urban forest stands, not only by exotic invasive trees but also by understory species (data not shown), suggests possible invasive meltdown, where introduced species facilitate the spread of new exotic species (Meltdown hypothesis; Simberloff 2006). Exotic species may alter soil communities potentially changing plant-soil feedback interactions of the native plant community (Mutualism disruption; Mitchell et al. 2006; Toby Kiers et al. 2010).

Despite the high amount of pathogens present in the roots of the exotic invasive species *R. cathartica* compared with the other target species, *R. cathartica* is a successful invader of the sampled stand. This result is consistent with a previous study by Siemann and Rogers (2006) who found high levels of chewing injuries on seedling leaves in this species. When Siemann and Rogers (2006) eliminated herbivory using an insecticide they found that seedling growth was strongly promoted. Although we were unable to eliminate belowground herbivory in our experiment, we postulate that root pathogens may slow down invasion by *R. cathartica* thereby contributing to promoting its coexistence with other native and exotic species.

Insights and perspectives

We show that a consistently supported ecological mechanism that explains plant species coexistence in many ecosystems such as grasslands (Petermann et al. 2008), tropical, deciduous and montane forests (Martin and Canham 2010; Matthesius et al. 2011; Wright 2002), is not consistently supported for dominant native tree species in an invaded urban forest ecosystem. Many studies show that invasive exotic species disturb soil biota and fertility (Ehrenfeld 2003; Ehrenfeld 2010). As a result, there is disruption of the species co-existence mechanisms driven by soil biota, which leads to invasive species dominance to the detriment of native species. The fact that we found and increase in *A. platanoides* seedling biomass with distance from conspecific adult tree and a relatively high percentage of root pathogen injuries on the roots of the invasive *R. cathartica* supports that recruitment limitation and natural enemies interact to determine invasive species dominance (Siemann and Rogers 2006) and that native and exotic plant species may coexist in invaded forest ecosystems (Lugo 2004).

Further research on the mechanisms behind species coexistence and succession of invaded forest ecosystems is needed to design effective strategies to prevent invasion and conserve native biodiversity. Tracking the dynamics of plant communities, and their interactions (both below and aboveground) across consecutive successional stages is necessary since an invasive species that is abundant in the understory as a sapling may be outperformed by a native species in subsequent successional stages (Lugo 2004; Siemann and Rogers 2006). Urban forests are ideal systems to study the consequences of multiple exotic species introductions in forest ecosystems. Preventing invasions in urban forests is necessary to preserve the native diversity of major biomes since human centers embedded in natural areas are highly prone to exotic species invasions (Guirado et al. 2006; Loewenstein and Loewenstein 2005; McKinney 2006; Vilà and Ibáñez 2011) and act as a potential invasion pathway to natural ecosystems.

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