Plant functional shifts in the invaded range: a test with reciprocal forest invaders of Europe and North America

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Summary

1. Comparative trait analyses of native and invasive plant species have enriched our understanding of the strategies that make plants successful in particular contexts. However, it is generally unknown whether traits associated with invasiveness arise *de novo* in the introduced range or represent a case of 'pre-adaptation' of some species to become invasive.

2. We compared the functional strategies of two invasive species, *Prunus serotina*, a tree native to Eastern North America (ENA) and invasive in European forests, and *Rhamnus cathartica*, a shrub native to Europe and invasive in ENA, in both their native and invasive ranges. We measured leaf functional traits related to plant carbon and nitrogen economics in populations across northeastern ENA (New York) and northern France. This reciprocal field approach is unique, comparing *in situ* physiology within and between each species' shared ranges.

3. For both species, we found striking differences in leaf economic traits and intraspecific trait scaling relationships. *Prunus serotina* exhibited similar photosynthetic rates in New York (native range) and France (invasive range), but French populations had significantly greater leaf carbon investments in the form of increased leaf respiration, construction costs, and carbon concentrations. *Rhamnus cathartica* exhibited 50–60% higher photosynthetic rates in New York (invasive range) than France (native range), along with increased leaf nitrogen costs. New York populations also had significantly lower nitrogen resorption efficiency, with autumn leaf nitrogen concentrations 69% lower in France.

4. Intraspecific trait differences between native and invasive ranges indicate shifts in resource-use strategies between the native and invasive range are possible in invasive species. While further investigations with additional species would be needed to determine the role of phenotypic plasticity and prevalence of post-introduction trait shifts, our results question the assumption that functional strategies of invasive species are conserved from the native range and highlight the utility of measuring *in situ* functional strategies of reciprocal invaders to provide mechanistic understanding of invasions.

Key-words: biological invasions, introduced range, leaf economics spectrum, leaf nitrogen, native range, nitrogen resorption efficiency, nitrogen resorption proficiency, photosynthetic rate

Introduction

Research on plant invasions has increasingly focused on functional traits of non-native plant species in efforts to understand the physiological underpinnings behind invasion success (Daehler 2003; van Kleunen, Weber & Fischer 2010). Many studies have compared particular traits or coordinated trait syndromes (strategies) of invasive species in their introduced range with those common in the native resident flora, with invaders biased toward more productive traits, such as high photosynthetic capacities (A_{sat}), specific leaf area (SLA), and leaf nutrient investments (e.g., Leishman *et al.* 2007; Peñuelas *et al.* 2009; Tecco *et al.* 2010; Heberling & Fridley 2013; Ordonez & Olff 2013). Despite these advances, relatively few studies have addressed whether the functional strategies of invasive species change in their invaded range compared to those of

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their native range (Hierro, Maron & Callaway 2005; cf. Blossey & Nötzold 1995; Zou, Rogers & Siemann 2007; Leishman, Cooke & Richardson 2014).

Intraspecific home-and-away trait comparisons have several potential outcomes. First, a species might exhibit significantly different trait values or resource-use strategies in their invasive range compared to their native range, due to enemy release (e.g., reduced herbivory and/or resource reallocation towards growth) or a novel competitive environment (weak biotic resistance). This shift could be due to evolution in the new range (e.g., local adaptation, genetic drift, admixture, founder effects) and/or phenotypic plasticity. Alternatively, a species might possess similar ecophysiologies in both native and invasive ranges, indicating pre-adaptation and niche similarities between ranges (Fridley & Sax 2014). Lastly, both post-introduction evolution and pre-adaptation can occur jointly, where species or populations with particular pre-adapted traits successfully naturalize, with post-introduction evolutionary fine-tuning to local environments in the new range (e.g., Henery et al. 2010). A growing number of common garden seedling studies of native and invasive populations, primarily comparing morphological traits of herbaceous species, have demonstrated important shifts of invaders toward competitive phenotypes (e.g., Blossey & Nötzold 1995; Zou, Rogers & Siemann 2007; García et al. 2013). Fewer studies compare physiological strategy differences measured in native and invasive range habitats (Leishman, Cooke & Richardson 2014; Lamarque et al. 2015).

Here, we investigate range-level trait differences in north temperate deciduous forests in Europe and Eastern North America (ENA). Recent research on shrubs and lianas in ENA forests has demonstrated that woody invaders from a wide variety of taxonomic groups exhibit extended foliar phenology and contrasting resource-use strategies compared to woody native species. Compared to ENA native congeners, invasive species, which originate from East Asia or Europe, tend to senesce leaves later into the fall (Fridley 2012), possess higher photosynthetic abilities and resource-use efficiencies (Heberling & Fridley 2013) and exhibit lower leaf N resorption and root traits associated with more effective nutrient foraging (Jo, Fridley & Frank 2015). In an analysis of invasion patterns across the Northern Hemisphere, Fridley (2013) suggested that these forest invaders may have 'pre-adapted' traits in their native range that confer invasiveness in ENA. Invasion patterns indicate directionality toward ENA forest invasions by shade tolerant East Asian species. European species tend to be more invasive in disturbed/anthropogenic habitats, whereas ENA species tend to invade European and East Asian meadows. However, forest understories in Europe are not immune to invasion (e.g., Closset-Kopp et al. 2007). As European forests have a long anthropogenic history, ENA forests have also been increasingly modified through anthropogenic disturbances, including deer overpopulation (Côté et al. 2004), eutrophication (Aber et al. 1989), and non-native earthworm invasions (Bohlen et al.

2004), suggesting fitness advantages for species functional shifts toward more productive phenotypes in this environment. However, it is unclear if the functional strategies shown in introduced populations are consistent with those expressed in their native ranges.

To determine whether carbon (C) capture and resource-use strategies differ between native and invasive ranges, we measured *in situ* leaf-level C assimilation, energy and N investments, resource-use efficiencies and leaf N resorption strategies in two woody species found in north temperate deciduous forests, *Prunus serotina* (Rosaceae; black cherry) and *Rhamnus cathartica* (Rhamnaceae; common buckthorn). We sampled individuals from multiple populations of each species in Europe (northern France) and ENA (central New York, USA) across forest edge and understory environments. This transatlantic comparison is unique in that the two species are reciprocally invasive (i.e. one species is native where the other is invasive, and viceversa). Because the species occur in the same stands or within the same region in both areas, this approach helps disentangle trait responses due to particular regional conditions (e.g., climate, soil properties) vs. whether the species is invasive in the region.

Two explanations have been proposed to explain the general success of *P. serotina* in European forests. In its native range (ENA), high seedling mortality as a result of soil pathogens near mature trees limits population densities (Packer & Clay 2000). However, in Europe, this pathogen-mediated negative soil feedback is absent (Reinhart et al. 2003), which supports the enemy release hypothesis. Second, it has been suggested that *P. serotina* exhibits a unique mid-successional strategy with a relatively shade-tolerant, long-lived sapling bank but fast growth upon gap formation. This particular strategy is largely absent in the European flora but common in native range competitors, thereby conferring a demographic advantage in French forests (Closset-Kopp et al. 2007). As a result from release from soil pathogens and pre-adaptation, we hypothesized that invasive (French) populations should exhibit more productive traits (e.g., photosynthetic capacity) compared to those measured in the native range (ENA).

Similarly, we hypothesized that *R. cathartica* in the invaded range (ENA) should exhibit traits related to greater resource gain (e.g., leaf N, photosynthetic capacity) compared to populations sampled in similar habitats in the native range (France). In its invasive range, *R. cathartica* displays increased leaf N, greater photosynthetic capacity, extended leaf longevity and reduced leaf N resorption prior to fall leaf senescence compared to resident natives (e.g., Harrington, Brown & Reich 1989; Fridley 2012; Heberling & Fridley 2013; Jo, Fridley & Frank 2015). Knight (2006) hypothesized that the relatively high N in leaf litter (i.e. low N resorption proficiency) in ENA is related to its extended leaf lifespan into fall, as the timing of leaf senescence places physiological constraints on the efficiency of N resorption prior to abscission (Niinemets & Tamm 2005). This hypothesis would be supported if leaf N

resorption proficiency were greater in native European populations, where extended phenology has not been reported (Knight *et al.* 2007). Alternatively, as symbiotic N-fixing association with *Frankia* is an ancestral character in Rhamnaceae (but not exhibited by *R. cathartica*; Soltis *et al.* 1995), a relatively wasteful plant N economy often associated with N-fixers may be intrinsic to the clade. Indeed, non-native *R. cathartica* individuals showed similarly low N resorption proficiency to N-fixers compared with other non-N-fixing taxa (Stewart *et al.* 2008). This phylogenetic constraint hypothesis argues similar N conservation strategies in both native and invasive populations.

Materials and methods

STUDY SPECIES

Prunus serotina Ehrh. (Rosaceae; black cherry) is a mid-successional tree native to ENA and invasive throughout European forests. This gap-dependent species follows a "sit-and-wait" strategy, where it can form a relatively slow-growing, long-living, shade-tolerant sapling bank under closed canopy conditions. Upon gap formation, the species exhibits rapid growth and reproduction, and can resprout from stumps and roots to revert back to the shade tolerant stage (Closset-Kopp *et al.* 2007). It was introduced to Europe for ornamental purposes in the 17th century, became naturalized in the 19th century, and has been recognized as invasive since the mid 20th century (Starfinger 1997).

Rhamnus cathartica L. (Rhamnaceae; common buckthorn) is a large shrub or small tree native to Europe and western Asia and invasive across ENA (Knight *et al.* 2007). It is regarded as shade tolerant in both its native (Grubb *et al.* 1996) and invasive (Knight 2006) ranges. Introduced as early as the late 1700s (Kurylo & Endress 2012), buckthorn invades a diversity of habitats in ENA, including open fields, forest edges, and shaded understories. In contrast, despite its relative shade tolerance, it is primarily limited to open areas or forest edges in its native range (Kurylo *et al.* 2007).

SAMPLING PROTOCOL

Eight spatially separated populations of each species were sampled in ENA (New York state) and Europe (France) in June and July 2013 (Table S1 in Supporting Information). In ENA, we chose four locations in central New York ("NY"), USA where both species co-occur. As the two species rarely co-occur in Europe (i.e. found in the same forest), we chose four locations per species in France. However, all French populations were within the same general region and environmental conditions.

Ten individuals of each species were sampled per site. We sampled saplings of 1–2 m height for access to crown foliage. To the extent possible, individuals of each population were sampled equally across forest edge, gap and closed canopy understory conditions. To account for light-mediated trait variation, "Gap Light Index" (GLI; Canham 1988) was calculated using hemispherical photographs taken directly above the canopy of each individual (Gap Light Analyzer; Frazer, Canham & Lertzman 1999).

Gas exchange measurements were performed on cut branches, following the protocol of Niinemets *et al.* (2005), widely used for temperate woody species. Two upper branches per individual were cut in the field and immediately recut under water. To maintain xylem water potential, the severed ends were wrapped with wet paper towel, placed in plastic bags, and stored in a cooler to minimize transpiration until transported to the lab, typically within 2 h (for distant populations, within 4–6 h). Upon returning to lab, branches were recut and cut stems placed in water, loosely covered in transparent plastic, and stabilized at room temperature under low light for 1–3 days before recording gas exchange measurements. Each morning, branches were recut under fresh water. There was no indication of time effect on gas exchange during the measurement period. Protocol tests on other temperate woody species suggest most species exhibit consistent light saturated photosynthetic rates immediately following branch cutting, but stomatal conductance decline during longer measurement periods (Niinemets *et al.* 2005). We found dark respiration rates to be particularly variable 1 h after cutting and require 24 h to stabilize (unpublished data). While detached branches with leaves acclimated to low light in lab may subtly differ from day-to-day rates measured *in situ*, all individuals were treated in a consistent manner facilitating our within species comparisons.

LEAF GAS EXCHANGE

Gas exchange measurements were made on recently expanded, mature leaves using an LI-6400 portable photosynthesis system equipped with CO_2 and temperature control modules, 2×3 cm sample chamber and a red-blue LED light source (Li-Cor, Lincoln, NE, USA). Leaf temperature was maintained at 25 °C under ambient humidity throughout measurements with sample chamber flow rate of 500 µmol s^{-1} and sample chamber CO_2 concentration at 380 µmol mol^{-1}. Leaves were photoinduced at a moderate irradiance level (300 µmol photons m^{-2} s^{-1}) until equilibration. Light levels were then progressively increased until light saturation (800–1500 µmol photons m^{-2} s^{-1}). All individuals were light saturated at the highest light levels, with no apparent signs of photoinhibition. Light-saturated net photosynthetic rate (A_{sat}) was recorded after equilibrating for at least two minutes at each PPFD and reaching defined stability parameters based on photosynthetic rate and stomatal conductance to water. After achieving light saturation, light levels were decreased incrementally to 200 µmol photons m^{-2} s^{-1} and assimilation rate (A_{200}) was again recorded following equilibration. Lastly, the light source was shut off to measure daytime dark respiration (R_d). Due to light inhibition of respiration rate (Kok 1948) and diurnal variation, these R_d values represent an approximation of daytime dark respiration.

LEAF STRUCTURAL AND BIOCHEMICAL CHARACTERISTICS

Following gas exchange measurements, at least five leaves per branch were scanned for leaf area and oven dried at 60 °C for at least 48 h. Specific leaf area (cm^2 g^{-1}) was calculated as the leaf surface area per g dry mass. Ground leaf samples were placed in an ashing furnace at 500 °C for 4 h, and leaf ash concentration was calculated as ash mass divided by sample mass. Duplicate samples were averaged for each individual. Mass-based leaf nitrogen (N_{mass}) and carbon (C_{mass}) concentrations were determined using an elemental analyser (CE Elantech, Lakewood, NJ, USA) for leaves collected for photosynthetic measurements.

To measure leaf N resorption, recently senesced leaves were collected in autumn (October-November) on the same individuals by gently shaking the plant and collecting fallen leaves, aiming to collect leaves from the same cohort as the mature leaf collection. Senesced leaves were oven dried, weighed, and analysed for C and N. Because leaf mass loss and area shrinkage during senescence can be significant, using uncorrected nutrient concentrations in senesced tissue can lead to an underestimation in calculated nutrient resorption rates (van Heerwaarden, Toet & Aerts 2003). Therefore, mass loss was corrected following Vergutz *et al.* (2012). Senesced leaf N concentration (senesced N_{mass}) was calculated as

senesced $N_{mass} \times$ MLCF, where MLCF is the mass loss correction factor, calculated as the ratio of the dry mass of senesced leaves to the dry mass of mature leaves. Senesced N_{mass} is interpreted as the inverse of leaf N resorption proficiency (Killingbeck 1996). Similarly, the percent reduction of leaf N between mature and senesced leaves, leaf N resorption efficiency (NRE), was calculated as [1− (senesced N_{mass}/mature N_{mass})MLCF] × 100.

Leaf construction cost (CC) quantifies the amount of glucose equivalents required to construct a leaf in terms of carbon skeletons, reductant, and ATP, excluding additional costs for maintenance and substrate transport (Williams, Field & Mooney 1989). Leaf CC_{mass} (g glucose g^{-1} leaf mass) was determined using a biochemical approximation (Vertregt & Penning de Vries 1987; Poorter 1994; Boyd, Xu & Griffin 2009):

$$CC_{mass} = (-1.041 + 5.077C_{mass})(1 - 0.67Ash) + 5.325N_{mass}$$

where C_{mass} is leaf carbon concentration, Ash is leaf ash concentration (proxy for mineral concentration; Vertregt & Penning de Vries 1987), and N_{mass} is leaf nitrogen concentration (all in g g^{-1}). We assumed leaf NO_3^- accumulation is negligible compared to organic N forms, and nitrate is the dominant form of N uptake. The first part of the CC equation above takes into account the carbon costs (empirically determined from the relationship between glucose costs and C content of biochemical compounds; Vertregt & Penning de Vries 1987). The second part of the first term (including ash) subtracts the mineral component in organic tissue from C cost, as the mineral fraction in organic tissue does not require C skeletons and energy required for their uptake is independent of costs for growth (Poorter 1994). The last term of the CC equation above accounts for the additional, substantial costs required to reduce nitrate into organic N (proteins).

Resource-use efficiency (RUE) is broadly defined as the amount of carbon assimilated per unit resource (Funk & Vitousek 2007). Potential photosynthetic energy-use efficiency (PEUE) was calculated as $A_{sat,mass}/CC_{mass}$. Potential photosynthetic nitrogen-use efficiency (PNUE) was calculated as $A_{sat,mass}/N_{mass}$.

DATA ANALYSIS

Where necessary, measurements were converted between area (i.e. m^{-2} leaf) and mass-based estimates (i.e. g^{-1} leaf) through their corresponding SLA. All statistical analyses were performed in R (R Development Core Team 2014). Trait differences between regions were assessed with linear mixed-effect models (Bates *et al.* 2014) that accounted for population-level variation through random effects. To control for possible effects of light environment, GLI was included in all models as a fixed effect covariate. For each trait, we compared models with and without a fixed effect of region (native or non-native) using likelihood ratio tests, following a χ^2 distribution with one degree of freedom. When necessary, data were log-transformed to satisfy model assumptions. Bivariate relationships were analysed with standardized major axis (SMA; Warton *et al.* 2006) line fitting implemented with the *smatr* package in R (Warton *et al.* 2012).

Results

COMPARATIVE FUNCTIONING BETWEEN NATIVE AND INVASIVE RANGES

Both species showed significant functional trait differences between their native and invasive ranges (Table 1). However, the magnitude and direction of trait shifts were not consistent across ranges of each species. In general,

R. cathartica exhibited greater inter-population trait separation than *P. serotina*.

Rhamnus cathartica in New York ("NY;" invasive range) had significantly greater potential photosynthetic rates than French (native range) populations, at both low (A_{200}) and saturating ($A_{sat,mass}$; $A_{sat,area}$) light levels (Table 1). Leaf respiration rates ($R_{d,area}$, $R_{d,mass}$) were variable among individuals (Fig. 1a), but the region-level means were similar across ranges (Table 1). As expected with increased photosynthetic capacity, invasive NY populations had greater leaf N investments (N_{mass}, C:N; Table 1). Further, NY populations displayed much lower leaf N resorption proficiencies (i.e. higher senesced N_{mass}) and efficiencies (percent N_{mass} resorbed prior to leaf senescence; Table 1). Each population included a relatively wide range of leaf N resorption efficiencies, but NY populations were consistently lower (Fig. 2a). After including the effects of light environment on SLA ($r = -0.60$, $P < 0.001$), there was no indication of differences in C investment traits by region, although French populations invested more in leaf carbon relative to nitrogen than invasive NY populations (C:N, Table 1). There were no consistent inter-population differences in leaf construction costs (CC_{area}, Fig. 1c) or SLA (Fig. 1d).

In contrast, *P. serotina* showed nearly identical photosynthetic rates across invasive French and native NY populations (Table 1, Fig. 1e–h). Mean C gain rates ($A_{sat,mass}$; $A_{sat,area}$; A_{200}) for *P. serotina* were slightly lower in France (invasive) than NY(native), but these differences were on the order of 3–12% and statistically insignificant ($P > 0.1$, Table 1). Likewise, *P. serotina* exhibited similar N investments (N_{mass}, N_{area}, C:N) and resorption rates (Senesced N_{mass}, N resorption efficiency, Fig. 2b). However, unlike *R. cathartica*, *P. serotina* had significantly greater C investments in the sampled invasive range populations (France), including greater CC_{mass} and mass-based leaf C concentration (C_{mass}, Table 1). Respiratory costs ($R_{d,mass}$, $R_{d,area}$) were also greater in France compared to sampled individuals in native ENA.

CARBON GAIN TRADE-OFFS WITH RESOURCE INVESTMENTS

Considering bivariate cost-benefit trait trade-offs in $A_{sat,area}$ (C gain potential) with associated resource investments, *R. cathartica* exhibited strong intraspecific correlations (Fig. 1a–d), both within ranges and overall. In contrast, trait relationships were weak for *P. serotina* (Fig. 1e–h), with insignificant bivariate trends ($R^2 < 0.10$, $P > 0.1$). Results were broadly similar when traits were expressed on a mass-basis (Fig. S1).

Invasive *R. cathartica* exhibited greater C returns per increase in respiratory costs than native populations (slope shift in A_{sat}-R_d, Figs 1a and S1). Similarly, invasive *R. cathartica* populations were shifted further along a shared trade-off (slope) in the $A_{sat,area}$- N_{area} relationship (Fig. 1b) and $A_{sat,area}$-CC_{area} (Fig. 1c). Although there

Table 1. Mean values (±1 SE) by species for photosynthetic, biochemical, structural, and resource-use efficiency leaf traits among native and invasive ranges. Statistical differences between native and invasive populations were determined using likelihood ratio tests (χ^2 with 1 df) that compared models for each trait with and without a fixed effect of range (invasive or native) with light environment as a fixed effect and population as a random factor. Region-level means do not adjust for potential light environment effects

Trait (units)†	*Prunus serotina* (PRSE)			*Rhamnus cathartica* (RHCA)		
	Invasive (France)	Native (New York)	Native status (χ^2)	Invasive (New York)	Native (France)	Native status (χ^2)
$A_{sat,area}$ (μmol CO_2 m^{-2} s^{-1})	5·96 ± 0·31	6·59 ± 0·38	0·34	10·75 ± 0·86	6·52 ± 0·43	4·00*
$A_{sat,mass}$ (nmol CO_2 g^{-1} s^{-1})	161·9 ± 10·6	185·9 ± 11·1	0·52	**296·3 ± 13·8**	**189·5 ± 11·5**	7·58**
$A_{200,area}$ (μmol CO_2 m^{-2} s^{-1})	4·45 ± 0·20	5·03 ± 0·21	1·72	**6·57 ± 0·27**	**4·98 ± 0·31**	4·74*
$R_{d,area}$ (μmol CO_2 m^{-2} s^{-1})	**0·65 ± 0·05**	**0·40 ± 0·04**	7·44**	0·37 ± 0·05	0·51 ± 0·05	0·24
$R_{d,mass}$ (nmol CO_2 g^{-1} s^{-1})	**16·3 ± 1·0**	**11·3 ± 0·8**	8·99**	10·7 ± 0·7	14·4 ± 1·3	0·66
SLA (cm^2 g^{-1})	263·2 ± 13·9	301·2 ± 10·5	0·10	323·6 ± 20·4	287·6 ± 7·4	0·62
Mature N_{mass} (%)	2·79 ± 0·10	2·91 ± 0·07	0·17	**3·92 ± 0·10**	**3·11 ± 0·11**	7·69**
Mature N_{area} (g m^{-2})	1·21 ± 0·10	1·02 ± 0·04	<0·01	1·41 ± 0·09	1·10 ± 0·04	2·87$^+$
Mature C:N	18·60 ± 0·73	16·18 ± 0·43	1·19	**11·71 ± 0·32**	**15·31 ± 0·63**	7·40**
Senesced N_{mass} (%)	1·32 ± 0·11	1·36 ± 0·07	<0·01	**2·86 ± 0·08**	**1·69 ± 0·04**	22·38***
N resorption efficiency (%)	58·43 ± 4·18	61·83 ± 2·47	0·09	**34·06 ± 2·03**	**48·96 ± 2·75**	9·50**
Mature C_{mass} (%)	**49·44 ± 0·16**	**46·17 ± 0·48**	6·65**	44·74 ± 0·26	45·29 ± 0·23	1·42
Mature C_{area} (g m^{-2})	21·15 ± 1·25	16·46 ± 0·78	0·53	16·92 ± 1·26	16·15 ± 0·40	<0·01
Ash (mg g^{-1})	**50 ± 1**	**66 ± 2**	5·46*	106 ± 3	108 ± 3	<0·01
CC_{mass} (eq. g glucose g^{-1})	**1·567 ± 0·009**	**1·400 ± 0·025**	8·93**	1·349 ± 0·016	1·334 ± 0·015	0·25
CC_{area} (eq. g glucose m^{-2})	65·92 ± 4·00	50·00 ± 2·49	3·16$^+$	51·03 ± 3·93	47·52 ± 1·22	0·02
PNUE (μmol CO_2 g^{-1} N s^{-1})	6·22 ± 0·51	6·46 ± 0·35	0·10	**7·63 ± 0·35**	**5·16 ± 0·41**	5·61*
PEUE (μmol CO_2 kg^{-1} glucose s^{-1})	103·58 ± 7·07	133·88 ± 8·38	1·89	**220·25 ± 11·01**	**123·19 ± 10·00**	8·09**

Significantly different values ($P < 0.05$) by range are indicated in bold.

†$A_{sat,area}$ and $A_{sat,mass}$, area- and mass-based light saturated net photosynthetic rate ($A_{sat,mass} = A_{sat,area} \times$ SLA); $A_{200,area}$, area-based net photosynthetic rate at lower photosynthetic photon flux density (200 μmol photons m^{-2} s^{-1}); $R_{d,area}$ and $R_{d,mass}$, area- and mass-based dark respiration rate; SLA, specific leaf area; Mature N_{mass} and N_{area}, mass- and area-based leaf nitrogen concentration of mature foliage; Senesced N_{mass}, mass-based terminal leaf nitrogen concentration of freshly abscised leaves in autumn; C_{mass} and C_{area}, mass- and area-based leaf carbon concentration; Ash, leaf ash concentration; CC_{mass} and CC_{area}, mass- and area-based leaf construction costs; PNUE, photosynthetic nitrogen use efficiency; PEUE, photosynthetic energy use efficiency.

$^+$$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

were no range-level mean differences in SLA (Table 1), at a given SLA, individuals measured in NY had consistently greater $A_{sat,area}$ than those in native France.

In addition to mid-season mature leaf N (N_{area}, N_{mass}), maximum photosynthetic rate ($A_{sat,mass}$) was closely correlated to N concentration in senesced leaves (senesced leaf N_{mass}) in both species (Fig. 3). As expected from N resorption efficiency differences (Fig. 2), invasive *R. cathartica* was shifted along a common slope, with both greater $A_{sat,mass}$ and greater senesced N_{mass} (Fig. 3a). In contrast, there were no scaling differences in this relationship for *P. serotina*, despite significant trait correlation (Fig. 3b).

RANGE-LEVEL DIFFERENCES IN INSTANTANEOUS RESOURCE-USE EFFICIENCIES

Although invasive populations exhibited consistently greater A_{sat} (*R. cathartica*) and leaf CC (*P. serotina*), only *R. cathartica* displayed differences in nitrogen and energy-use efficiencies. Mean photosynthetic nitrogen-use efficiency (PNUE) was greater in NY for invasive *R. cathartica*, despite lower N investments in French populations (Table 1, Fig. 3a). Also, as a result of greater A_{sat} in NY

than France, but with similar CC, photosynthetic energy-use efficiency (PEUE) was greater in NY (Table 1).

Discussion

DO SPECIES FOLLOW DIFFERENT RESOURCE-USE STRATEGIES IN THEIR INVASIVE RANGES?

Our current understanding of the functional ecology of invasive plants has largely been informed from studies that compare non-native species with co-occurring native species (van Kleunen, Weber & Fischer 2010). These interspecific contrasts often highlight trait-based strategy differences, including those associated with increased carbon capture abilities (e.g., Leishman, Thomson & Cooke 2010; Heberling & Fridley 2013), faster growth rates (e.g., Grotkopp, Rejmánek & Rost 2002), greater nutrient demands (e.g., Peñuelas *et al.* 2009), or higher resource-use efficiencies (e.g., Funk & Vitousek 2007; Heberling & Fridley 2013). However, it remains unknown whether the traits that confer greater relative plant success in their invasive range are similarly observed in their native range.

We measured *in situ* leaf traits of *P. serotina* (black cherry; invasive in France, native in ENA) and *R. cathartica*
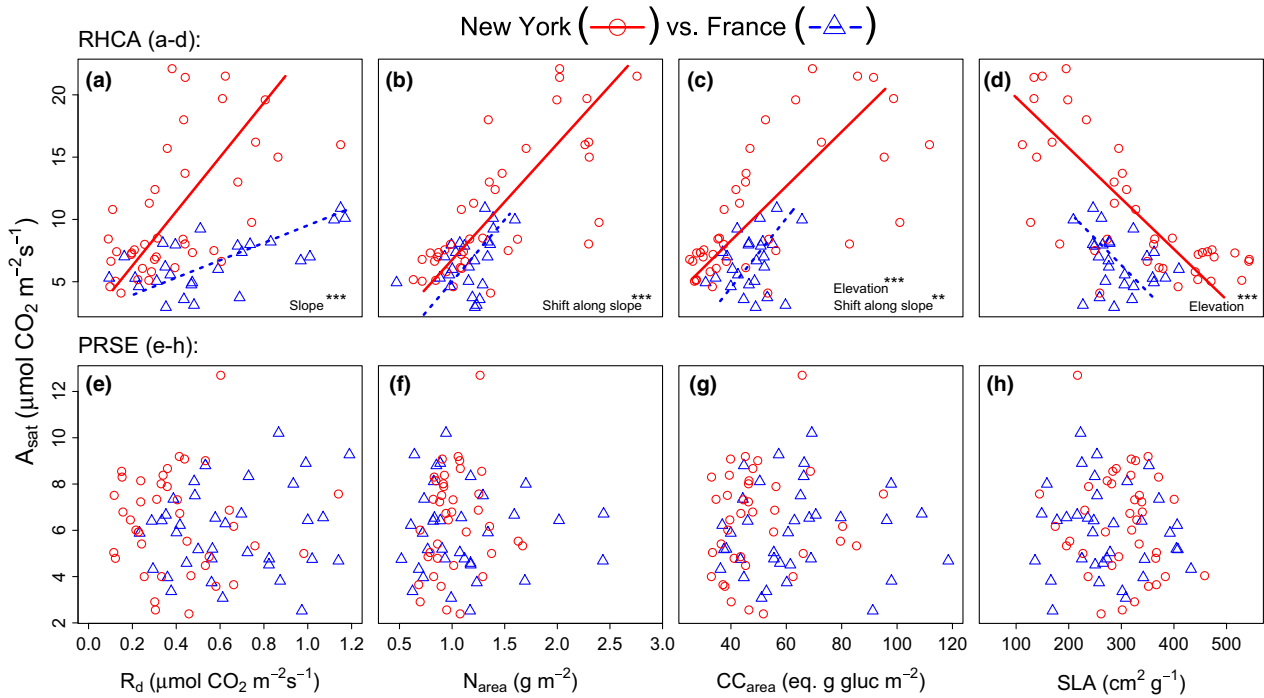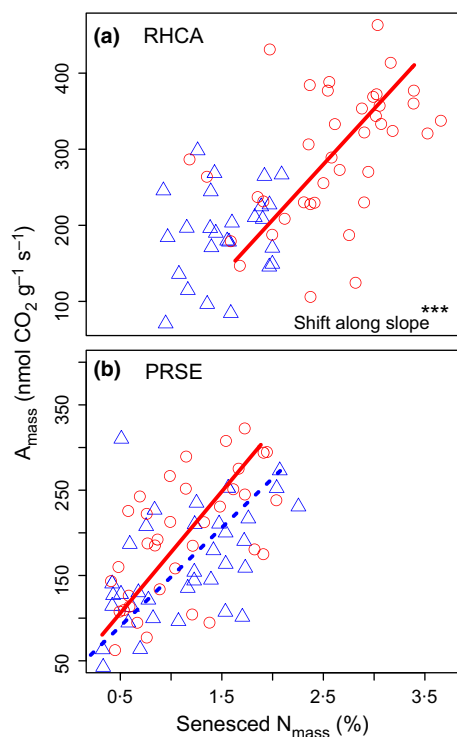
Fig. 1. Standardized major axis (SMA) relationships for area-based light saturated photosynthetic rate (A_{sat}) and leaf cost traits (a, e) dark respiration ($R_{d,area}$), (b, f) nitrogen concentration (N_{area}), (c, g) construction cost (CC_{area}) and (d, h) specific leaf area (SLA). *Rhamnus catharctica* (RHCA, a–d) and *Prunus serotina* (PRSE, e–h) individuals are plotted by region: New York (red circles, solid line); France (blue triangles, dashed line). SMA analyses performed only for relationships showing at least moderate correlation ($R^2 > 0.10$, $P < 0.1$). Significance tests indicate differences in slope, elevation (y-intercept), or shift along common slope (**$P < 0.01$, ***$P < 0.001$). (a) overall: $R^2 = 0.10$ $P < 0.01$; invasive: $R^2 = 0.33$, $P < 0.001$; native: $R^2 = 0.38$, $P < 0.001$ (b) overall: $R^2 = 0.54$, $P < 0.001$; invasive: $R^2 = 0.57$, $P < 0.001$; native: $R^2 = 0.15$, $P = 0.06$ (c) overall: $R^2 = 0.39$, $P < 0.001$; invasive: $R^2 = 0.46$, $P < 0.001$; native: $R^2 = 0.08$, $P = 0.18$ (d) overall: $R^2 = 0.35$, $P < 0.001$; invasive: $R^2 = 0.55$, $P < 0.001$; native: $R^2 = 0.09$, $P = 0.14$ (e–h) all $R^2 < 0.10$, $P > 0.1$.
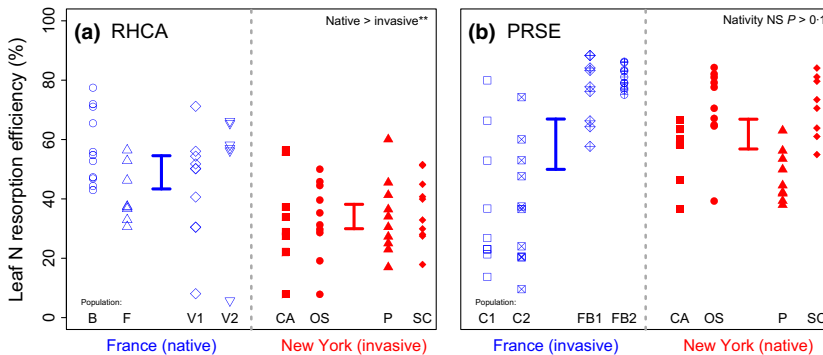
Fig. 2. Leaf N resorption efficiencies (NRE) by native- and invasive-range populations for (a) *Rhamnus catharctica* (RHCA) and (b) *Prunus serotina* (PRSE). Acronyms denote each population. Points indicate individual measurements. Error bars represent 95% confidence intervals for each range-level mean. Statistical differences between native and invasive ranges for each species were evaluated from likelihood ratio tests of linear mixed models that include population random effects (**, $P < 0.01$).

(common buckthorn; invasive in ENA, native in France) to test whether these species exhibit similar traits in their native ranges, or alternatively, if resource-use strategies differ in the invaded range. We hypothesized that both species would display traits that confer a more productive strategy in their invasive range. Our results strongly support the notion that invasive species follow different resource-use strategies in their native and invasive ranges. Interestingly, the nature of these trait shifts was not consistent between the two species studied, with invasive *P. serotina* populations in France shifted towards increased carbon investments and invasive *R. catharctica* in NY shifted towards increased carbon gains and nitrogen demands.

We hypothesized that *P. serotina* would have greater metabolic rates in its invasive range (France), due to escape from native soil pathogens absent in Europe that increase seedling mortality in North America (Reinhart *et al.* 2003). Contrary to this hypothesis, *P. serotina* showed similar maximum photosynthetic rates (A_{sat}) across regions (Table 1, Fig. 1e–h). Unexpectedly, relative to NY, invasive populations in France exhibited greater leaf CC_{mass} and leaf C_{mass}, indicating increased leaf energy investments. Additionally, we found average increases of 44% and 63% in area- and mass-based leaf respiration rates (R_d), respectively. Greater carbon investments might translate to increased leaf longevity and greater carbon assimilation when integrated over the growing season, and

Fig. 3. Standardized major axis (SMA) relationships for mass-based light-saturated photosynthetic rate ($A_{sat,mass}$) and leaf N in senesced leaves (senesced N_{mass}) for New York (red circles, solid line) and French (blue triangles, dashed line) individuals. (a) *Rhamnus catharticus* (RHCA): overall $R^2 = 0.40$, $P < 0.001$; France $R^2 = 0.05$, $P = 0.26$; ENA $R^2 = 0.21$, $P < 0.01$ (b) *Prunus serotina* (PRSE): overall $R^2 = 0.29$, $P < 0.001$; France $R^2 = 0.26$, $P < 0.01$; ENA $R^2 = 0.37$ $P < 0.001$. Significance tests indicate differences in slope, elevation (y-intercept), and shift along common slope (***$P < 0.001$).

explain the persistent, shade-tolerant sapling banks of *P. serotina* in invaded French forests, which have been interpreted as a unique ecological strategy in the context of the European tree flora (Closset-Kopp *et al.* 2007).

Further, we hypothesized that *R. catharticus* in its invasive range (ENA) should display increased photosynthetic rates, at the expense of high leaf nitrogen costs, which have been reported in ENA relative to co-occurring natives (Knight *et al.* 2007; Heberling & Fridley 2013). Our results support this prediction. Range-level differences were striking, with nearly 56% and 64% higher light-saturated photosynthetic rates in NY relative to France for $A_{sat,mass}$ and $A_{sat,area}$, respectively (Table 1, Fig. 1a–e). Further, NY populations exhibited increased gains per unit respiratory costs compared to French plants (A_{sat}-R_d slope shift, Fig. 1a), which has been previously reported for invasive species compared to co-occurring natives (Pattison, Goldstein & Ares 1998; McDowell 2002). In other words, per unit growth or maintenance respiratory cost, New York plants exhibited increased photosynthetic benefits. Additionally, NY invasive individuals invested more in leaf N, with appreciably lower leaf N resorption efficiency and proficiency (Fig. 2). Despite this, PNUE was greater in the

invaded range due to larger proportional increases in A_{sat}. A fundamental trade-off between high leaf nutrient acquisition and low internal conservation is predicted by plant resource-use strategy theory (Aerts & Chapin 1999) and has been supported in global analyses (Kobe, Lepczyk & Iyer 2005; Vergutz *et al.* 2012). Further, mid-season A_{sat} and fall senesced N_{mass} (inverse of nutrient proficiency) were closely correlated in both species (Fig. 3.). No differences were detected for *P. serotina* in this trade-off, while *R. catharticus* in ENA was shifted further along a common trade-off, with greater A_{sat} and N in senesced leaves (Fig. 3a).

Inconsistency in plant functional trait shifts from the native to invasive range was also found in other recent studies. On the one hand, Leishman, Cooke & Richardson (2014) measured leaf traits in populations across multiple ranges of 13 invasive species in the Southern Hemisphere and found trait shifts in the invasive populations toward faster growth strategies associated with reduced leaf herbivory. In contrast, Ordonez (2014) analysed literature-derived species trait values for species measured in native and introduced ranges and found large variation in the direction and magnitude of differences, with both increased and decreased trait values in their invasive ranges. Similarly, another meta-analysis, including both plants and animals, reported that individuals had higher mean performance traits (e.g., biomass) than in the invaded range, but noted that nearly the same number of species exhibited no change (Parker *et al.* 2013). Results of the present study further the expectation of functional trait shifts in the invasive range, but do not support the claim that such shifts should always be in the direction of greater productivity.

WHY ARE IN *SITU* RESOURCE-USE STRATEGIES DIFFERENT IN THE INTRODUCED RANGE?

Despite our findings of significant functional differences in the invaded range, it is unclear whether these trait shifts primarily result from pre-adaptation/post-introduction evolution or environmental variation. The design of a reciprocal invasion can explain potential functional trait shifts due to pre-adaptation and post-introduction effects, but not phenotypic plasticity. Environmental differences might be important, including climate (oceanic France vs. continental ENA), site edaphic characteristics, and photoperiod. Further, genetic variation across the range and the potential for founder effects from source populations may be also be important, as both species possess large native geographic distributions (Knight *et al.* 2007; Pairon *et al.* 2010). One possibility is that we have not captured the entire functional trait space exhibited by all populations, as we have only sampled a portion of the species' native and invasive ranges. Genetic studies indicate multiple introductions of *P. serotina* in Europe from Northeastern US populations (Pairon *et al.* 2010), in the general region we have sampled. Source populations for

R. cathartica introduction to ENA are less clear, but given the species' early introduction and widespread planting (Kurylo & Endress 2012), multiple source populations are possible. While our conclusions are limited our sampling, we find trait shifts between native and invasive populations growing in similar forests.

Another possible mechanism for the shift of *R. cathartica* toward greater assimilation rate through higher leaf N content in ENA is that the central NY region has generally higher soil N availability than northern France. Although we are limited in our interpretation of such differences due to lacking N supply data, we suggest soil fertility cannot be a full explanation for population differences, because: (i) leaf function and whole-plant productivity in central NY forests does not vary along experimental N gradients (Heberling & Fridley, unpublished); (ii) *P. serotina* populations growing in both regions did not display differences related to N economy, as would be expected if soil N differences were significant; and (iii) high leaf N in *R. cathartica* has been documented across its invasive range, involving a large variety of soil substrates (Knight *et al.* 2007; Kurylo *et al.* 2007).

In the native range, *P. serotina* densities are suppressed through high soil pathogen-mediated mortality in seedlings near mature trees (Reinhart *et al.* 2003). Although soil-borne pathogens have been suggested to suppress juvenile growth (Packer & Clay 2003), our lack of decreased photosynthetic function in NY compared to France indicate limited effects of pathogen attack on the physiology of the saplings we measured. Likewise, the high population densities observed in France likely do not translate to individual-level growth. Further, *P. serotina* occupies a particular mid-successional niche that may be absent in the European tree flora (Closset-Kopp *et al.* 2007), which suggests pre-adaptation. Higher leaf construction costs, carbon concentrations, and leaf respiration rates in French populations may facilitate the successful growth strategy of a long-lived, understory sapling stage in the invaded range.

In ENA, *R. cathartica* invades open sites, forest edges, and shaded forest understories. Interestingly, the species is primarily considered a forest edge species in Europe (Kurylo *et al.* 2007), despite its moderate shade tolerance (Grubb *et al.* 1996). Compared to native ENA species, *R. cathartica* exhibits extended leaf phenology (Harrington, Brown & Reich 1989; Fridley 2012), high photosynthetic rates, high leaf N (Heberling & Fridley 2013), and low leaf N resorption (Jo, Fridley & Frank 2015). However, in Europe, the phenology of *R. cathartica* does not differ appreciably from co-occurring natives (Knight *et al.* 2007) nor is it considered to have long lasting leaves compared to other European shrubs (Kollmann & Grubb 1999). Lower nitrogen resorption efficiency (Fig. 2a) and proficiency (Fig. 3a) in NY compared to France supports the prediction of Knight (2006), who hypothesized that the extended phenology strategy in ENA inhibits nutrient resorption prior to fall senescence. Lower N resorption in ENA may be a plastic response or selected trait for increasing leaf longevity and C gain.

Why would a low N conservation strategy for *R. cathartica* be advantageous in ENA, but not Europe? Several studies have associated *R. cathartica* invasions with a local abundance of non-native earthworms, which may promote a more wasteful plant N economy through altering N mineralization rates (Heneghan, Steffen & Fagen 2007; Madritch & Lindroth 2008; Roth *et al.* 2015). However, as earthworms are native in Europe, their presence in ENA alone cannot explain range-level trait differences. Similarly, temperate forests across both regions have been subjected to increased rates of anthropogenic N deposition (Galloway *et al.* 2004; Holland *et al.* 2005). Compared to native shrubs and lianas, other ENA invasive species with extended leaf phenology also showed higher rates of N uptake and lower resorption (Jo, Fridley & Frank 2015). Our results indicate this strategy of low N conservation is not present in the native range. Given the prevalence of this strategy in ENA forest invaders (Jo, Fridley & Frank 2015), N-based shifts in plant resource economy between ranges might be a more general, but unexplored, phenomenon.

Conclusions

We found that invasive species adopt different resource-use strategies in their invaded and native ranges. Such large divergences highlight the importance of considering intraspecific variation in functional trait analyses (Donovan *et al.* 2014; Niinemets 2015) and question the assumption that species mean trait values are conserved across native and invasive ranges (Ordonez 2014). The degree to which these range-level differences are genetic vs. plastic remains unknown. Rapid trait evolution in plant invasions is more common than previously thought (Buswell, Moles & Hartley 2011), but given the geographic ranges of many invasive species span large environmental gradients and biotic contexts, phenotypic plasticity likely plays a role in range-level differences. Common garden studies are needed to assess the roles of pre-adaptation, evolution, and plasticity in generating range-level differences. Additional comparisons with more species are needed to assess the prevalence of trait shifts. Nonetheless, our results provide an important step toward establishing and understanding how resource-use strategies found in the invaded range compare to those in the native range.

Acknowledgements

Data accessibility

The complete trait data set is available in Table S1.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Figure S1. Bivariate relationships by range for mass-based leaf traits.

Table S1. Leaf trait data set and associated metadata.