Resource-use strategies of native and invasive plants in Eastern North American forests

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Summary

- Studies in disturbed, resource-rich environments often show that invasive plants are more productive than co-occurring natives, but with similar physiological tradeoffs. However, in resource-limited habitats, it is unclear whether native and invasive plants have similar metabolic constraints or if invasive plants are more productive per unit resource cost – that is, use resources more efficiently.
- Using a common garden to control for environment, we compared leaf physiological traits relating to resource investments, carbon returns, and resource-use efficiencies in 14 native and 18 nonnative invasive species of common genera found in Eastern North American (ENA) deciduous forest understories, where growth is constrained by light and nutrient limitation.
- Despite greater leaf construction and nitrogen costs, invaders exhibited greater instantaneous photosynthetic energy-use efficiency (PEUE) and marginally greater photosynthetic nitrogen-use efficiency (PNUE). When integrated over leaf lifespan (LL), these differences were magnified. Differences in efficiency were driven by greater productivity per unit leaf investment, as invaders exhibited both greater photosynthetic abilities and longer LL.
- Our results indicate that woody understory invaders in ENA forests are not constrained to the same degree by leaf-based metabolic tradeoffs as the native understory flora. These strategy differences could be attributable to pre-adaptation in the native range, although other explanations are possible.

Introduction

Nonnative plant invasions are common in environments of anthropogenic disturbance (Hobbs & Huenneke, 1992), which has led to the generalization that nonnative invaders (hereafter 'invaders') are most likely to outperform native species in disturbed habitats with high resource availability (e.g. Daehler, 2003). Mechanisms attributed to these disturbance-mediated invasions include broad physiological advantages of invaders over natives following episodic increases in resource availability (Davis *et al.*, 2000). If these resource-based mechanisms are true, then invaders should exhibit advantages in functional traits that contribute to high productivity given ample resources, such as high specific leaf area, photosynthetic ability, and relative growth rate compared with native competitors (van Kleunen *et al.*, 2010; Drenovsky *et al.*, 2012). However, it remains unclear if invasion success in resource-limited ecosystems can be explained by mechanisms described for high-resource environments.

Over the past 15 yr, there has been substantial development of plant strategy theory and resource-use economics (Reich *et al.*, 1997; Westoby *et al.*, 2002; Wright *et al.*, 2004, 2005). Wright *et al.* (2004) reported a global pattern of coordinated variation in leaf traits ('worldwide leaf economic spectrum' (LES)) that invokes general ecophysiological tradeoffs in resource economics as a global axis of variation in plant strategies. This spectrum of strategic variation describes species from those with slow returns on investments (possessing traits such as low specific leaf area, high construction costs, low photosynthetic rates, and high leaf lifespan) to those at the opposite extreme of quick returns on resource investments. Strategies that lie outside of this general LES are presumed to either be selected against (ecologically constrained by biotic interactions) or biophysically or genetically impossible (Reich *et al.*, 1999; Donovan *et al.*, 2011).

In an effort to understand invasion processes in light of these developments, studies have explicitly placed invasive plants along a spectrum of leaf trait variation that emphasizes coordinated variation among leaf traits (e.g. Leishman *et al.*, 2007, 2010; Ordonez *et al.*, 2010; Peñuelas *et al.*, 2010; Ordonez & Olff, 2013). In particular, Leishman *et al.* (2010) argued that native and invasive plants share similar carbon (C) capture strategies, with invaders subject to the same tradeoffs between physiological investments and returns (i.e. constrained within the same LES). They concluded that, although invasive plants found in disturbed sites had traits that conferred greater productivity, they also experienced higher resource costs relative to natives. Therefore, invasive plants have strategies that correspond to the early successional, fast investment return portion of the LES, a conclusion

used to mechanistically explain their dominance in disturbed, high-resource ecosystems (Leishman *et al.*, 2007, 2010).

However, ecosystems subject to strong resource limitation are not immune to invasion (Martin *et al.*, 2009), including Eastern North American (ENA) deciduous forests that experience very low light and nutrient levels during the growing season (Fridley, 2008). It is an open question as to whether invasion mechanisms described for high-resource environments, such as old fields, anthropogenic sites, and roadsides, are applicable to less disturbed ecosystems of low resource availability (Funk & Vitousek, 2007). It is generally understood that species adapted to resource-poor habitats follow strategies that place a higher premium on efficient use of resources (conservative strategies) at the expense of rapid growth (Aerts & Chapin, 1999).

Demographic studies of temperate forest tree invasions suggest that invaders do not necessarily follow demographic or life history tradeoffs evident in the native flora, such as that between low-light survivorship and high-light growth (Martin *et al.*, 2010) and between classic *r*/*K* strategies of fast growth and reproduction versus persistence (Closset-Kopp *et al.*, 2007). Select comparative studies, often in habitats of limited light or nutrients, report invasive plants with seemingly superior performance compared with natives at a given metabolic or resource cost, including increased growth rates (Osunkoya *et al.*, 2010), greater mean performance or trait plasticity (Funk, 2008; Godoy *et al.*, 2012; Paquette *et al.*, 2012), greater photosynthetic rates at lower respiratory costs (Pattison *et al.*, 1998; McDowell, 2002) and greater resource- or energy-use efficiencies (Baruch & Goldstein, 1999; Nagel & Griffin, 2004; Funk & Vitousek, 2007; Boyd *et al.*, 2009). All else being equal, these findings imply that invasive species are not constrained by the same tradeoffs as natives, leading to greater production given similar resource investments. It remains unclear why these seemingly more efficient adaptations are not evident in neighboring native species. Phylogenetic constraints may exist, with certain floras never evolving certain trait combinations, which can explain how certain nonnative plants with novel resource-use strategies are superior competitors in a new range (Mack, 2003). A recent global analysis of leaf traits supports the possibility that evolutionarily distinct floras within similar biomes may have evolved different tradeoffs in resource capture strategies (Heberling & Fridley, 2012).

In ENA, the naturalized flora includes European forbs that inhabit open, managed, and disturbed sites. By contrast, invasive plants in ENA (i.e. those of highest management concern) are primarily woody species from Central and East Asia that are often invasive in forested habitats (Fridley, 2008). These shade-tolerant plants are particularly troublesome for management because their populations may increase as succession proceeds (Martin *et al.*, 2009). In a recent common garden study of ENA forest species, Fridley (2012) found that invaders exhibit systematic differences in growth phenology, with significantly later leaf senescence for invasive species. It is unclear if any fitness advantage of an extended growing season for invasive species is equalized by tradeoffs at the leaf level such as shorter lifespan (i.e. more rapid leaf turnover) or lower daily productivity.

To test whether invasive plants in ENA forests exhibit different patterns of resource use from natives, we measured leaf-level C gains, energy and nitrogen (N) investments, and resource-use efficiencies (RUEs) of invasive and native shrubs and lianas found in ENA deciduous forests. All plants were grown in a common garden to concentrate on intrinsic trait differences, rather than those that might arise from environmental differences. We expanded upon other invasion studies (e.g. Leishman *et al.*, 2010) to focus on phylogenetically related groups of species found in resource-limited habitats and considered both instantaneous and time-integrated traits (e.g. Funk & Vitousek, 2007). As ENA understory species are constrained by both light and N availability (Aber *et al.*, 1993; Finzi & Canham, 2000), we hypothesized that ENA invaders should have greater C gains at lower resource costs. Therefore, we predicted that invasions in ENA forests are not attributable to greater resource use than natives *per se*, but rather, greater efficiency in the use of those limiting resources (i.e. greater C gains per unit resource cost).

Materials and Methods

Species selection and sampling protocol

We studied 32 shrub and liana species (14 native and 18 nonnative), with 14 nonnative species formally recognized as 'invasive' in ENA deciduous forests and the remaining four recognized as 'naturalized' (Fridley, 2008; Table 1). 'Naturalized' refers to nonnative species capable of maintaining natural populations without human intervention, whereas 'invasive' species refers to a subset of naturalized species with actively spreading populations that have been formally recognized by management agencies. Removing naturalized, but not (yet) invasive, species from the analysis did not affect conclusions (analysis not shown). Therefore, the nonnative group is hereafter referred to as 'invasive' for simplicity. Because invasive forest species in ENA are biased toward those of East Asian origin (Fridley, 2008), these species were the focus for comparison to native congeners. While the studied species are not equally abundant across ENA, many can co-occur and all species occur in the understory across the Eastern Deciduous Forest biome. Plant material was collected from an experimental garden in Syracuse, New York, USA (43°03′N, 76°09′W) established in 2006 in three replicate blocks and a seasonal shade treatment (80%) to simulate forest understory light regimes (see Fridley, 2012). Individuals were originally collected from the wild in the Syracuse region or, if unavailable, acquired commercially from nurseries in North America of similar latitude (Supporting Information Table S1).

From July to mid-August 2011, two to six individuals per species were sampled from the common garden for subsequent measurements (mean ± SD: 3.22 ± 1.13 individuals per species). Gas exchange measurements were performed on cut branches, following the protocol of Niinemets *et al.* (2005). We used cut branches for logistical reasons and to ensure that measurements were made under consistent environmental conditions. On cool mornings between 06:00 and 08:00 h, two upper branches per individual were cut under water. To maintain xylem water

Table 1 Woody, deciduous species measured in this study, including current status in Eastern North America (Fridley, 2008), general growth form, and biogeographic origin

Family	Species	Invasive status	Growth form	Origin
Berberidaceae	*Berberis canadensis* Mill.[a]	Native	Shrub	
	Berberis koreana Palib.	Naturalized	Shrub	East Asia
	Berberis thunbergii DC.	Invasive	Shrub	East Asia
Caprifoliaceae	*Lonicera canadensis* J. Bartram ex Marshall	Native	Shrub	
	Lonicera fragrantissima Lindl. & Paxton	Invasive	Shrub	East Asia
	Lonicera hirsuta Eaton	Native	Liana	
	Lonicera involucrata (Richardson) Banks ex Spreng.	Native	Shrub	
	Lonicera japonica Thunb.	Invasive	Liana	East/Central Asia
	Lonicera maackii (Rupr.) Maxim.	Invasive	Shrub	East/Central Asia
	Lonicera morrowii A. Gray	Invasive	Shrub	East Asia
	Lonicera reticulata Raf.	Native	Liana/shrub	
	Lonicera sempervirens L.	Native	Liana	
	Lonicera standishii Jacques	Invasive	Shrub	East Asia
Celastraceae	*Celastrus orbiculatus* Thunb.	Invasive	Liana	East/Central Asia
	Celastrus scandens L.	Native	Liana	
	Euonymus alatus (Thunb.) Siebold	Invasive	Shrub	East Asia
	Euonymus americanus L.	Native	Shrub	
	Euonymus atropurpureus Jacq.	Native	Shrub/tree	
	Euonymus bungeanus Maxim.	Naturalized	Shrub/tree	East Asia
	Euonymus europaeus L.	Invasive	Shrub/tree	Eurasia
	Euonymus hamiltonianus Wall. ssp. *sieboldianus* (Blume) H. Hara	Naturalized	Shrub/tree	East/Central Asia
	Euonymus obovatus Nutt.	Native	Shrub	
	Euonymus phellomanus Loes.	Naturalized	Shrub	East Asia
Elaeagnaceae	*Elaeagnus angustifolia* L.	Invasive	Shrub/tree	Eurasia
	Elaeagnus commutata Bernh. ex Rydb.	Native	Shrub	
	Elaeagnus multiflora Thunb.	Invasive	Shrub	East Asia
	Elaeagnus umbellata Thunb.	Invasive	Shrub	East Asia
Lauraceae	*Lindera benzoin* (L.) Blume	Native	Shrub/tree	
Rhamnaceae	*Frangula alnus* Mill.	Invasive	Shrub/tree	Europe/Central Asia
	Frangula caroliniana (Walter) A. Gray	Native	Shrub/tree	
	Rhamnus alnifolia L'Hér.	Native	Shrub	
	Rhamnus cathartica L.	Invasive	Shrub/tree	Europe/Central Asia

[a]Taxonomic classification is unclear. Studied individuals may be hybrids of *Berberis canadensis* and *Berberis thunbergii*.

potential, the severed ends were retained in water and transported to the laboratory within 1 h. The branches were then recut under water and covered in transparent polyethylene plastic to reduce transpiration. Branches were stabilized at room temperature under low light for 1–2 d before recording gas exchange measurements. Each morning, branches were recut under water and the foliage was misted. This pre-conditioning period minimizes temporal and species-level differences in stomatal openness for comparable, consistent photosynthetic measurements (Niinemets *et al.*, 2005).

Leaf gas exchange

All gas exchange measurements were made in morning hours on recently expanded, mature leaves using an LI-6400 portable photosynthesis system equipped with CO_2 and temperature control modules (Li-Cor, Lincoln, NE, USA). Leaf temperature was maintained at 25°C under ambient humidity throughout measurements with a sample chamber flow rate of 700 µmol s^{-1}.

We measured leaf photosynthetic responses to irradiance (photosynthetic photon flux density (PPFD)) at 10 steps from 1000

to 0 µmol photons m^{-2} s^{-1} with sample chamber CO_2 concentration at 400 µmol mol^{-1}. All species were light saturated (without photoinhibition) at the highest light intensities. Net photosynthetic rate was recorded after equilibrating for at least 2 min at each PPFD and reaching defined stability parameters based on photosynthetic rate and stomatal conductance to water.

Light response curve parameters were estimated through nonlinear least squares regression of a nonrectangular hyperbola (Marshall & Biscoe, 1980):

$$A_{net} = \frac{\phi PPFD + A_{max} - \sqrt{(\phi PPFD + A_{max})^2 - 4\theta\phi PPFD(A_{max})}}{2\theta} - R_d$$

Eqn 1

(A_{net} and A_{max}, the area-based net and maximum gross photosynthetic rates (µmol CO_2 m^{-2} s^{-1}), respectively; ϕ, the apparent quantum yield (mol CO_2 mol photons^{-1}); R_d, the daytime dark respiration rate ($|A_{net}|$ at no light; µmol CO_2 m^{-2} s^{-1}); θ, curve convexity (dimensionless).) The light compensation point (LCP) was estimated from the *x*-axis intercept, and the

light saturation point (LSP) was estimated as the PPFD when 75% of A_{max} (model asymptote) was achieved.

Similarly, we measured leaf photosynthetic responses to changing intercellular CO_2 pressure (photosynthetic rate/intercellular CO_2 partial pressure (A/C_i) curves) by varying sample chamber CO_2 concentrations between 50 and 500 µmol CO_2 mol^{-1} while maintaining saturating PPFD. A/C_i measurements were taken from the same leaves (or from adjacent nodes) as those for light response curves. Following Wullschleger (1993), maximum carboxylation rates ($V_{c,max}$) were estimated from CO_2 response (A/C_i) curves when C_i was < 20 Pa (Rubisco limited). The biochemical photosynthetic model developed by Farquhar *et al.* (1980) was fitted using nonlinear least squares regression:

$$A_{net} = V_{c,max} \frac{C_i - \Gamma^*}{C_i + K_c(1 + O/K_o)} - R_{day} \text{ (when } C_i \leq 20 \text{ Pa)}$$

Eqn 2

(C_i, intercellular CO_2 partial pressure (Pa); K_c and K_o, Michaelis–Menten constants for carboxylation and oxygenation (40.4 Pa and 24.8 kPa, respectively); O, the O_2 concentration (21 kPa); $V_{c,max}$, the maximum carboxylation rate (µmol CO_2 m^{-2} s^{-1}); R_{day}, the daytime mitochondrial respiration rate (µmol CO_2 m^{-2} s^{-1}); Γ^*, the CO_2 compensation point in the absence of mitochondrial respiration (3.7 Pa).) Rubisco kinetic constants were obtained from von Caemmerer (2000). These constants were assumed to be similar among species (see Sharkey *et al.*, 2007). Calculations using an independent set of literature-derived kinetic constants did not affect the reported conclusions (analysis not shown).

Leaf structural and biochemical characteristics

Following gas exchange measurements, the leaves were harvested, pressed, and oven-dried at 60°C for at least 48 h. Leaf area was measured using a leaf area meter (LI-3100; Li-Cor) and scanned leaf images. 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 500ºC for 4 h, and leaf ash concentration was calculated as ash mass divided by sample mass. Duplicate samples were averaged for each individual. Leaf N and C concentrations were determined using an elemental analyzer (CE Elantech, Lakewood, NJ, USA) for leaves collected for photosynthetic measurements and, for a limited species subset, leaf litter samples collected after leaf fall. Leaf lifespan (LL) was determined from 2008 to 2010 biweekly leaf censuses as described in Kikuzawa (1983) and averaged over the years monitored for each species (Fridley, 2012).

Leaf construction cost (CC) quantifies the amount of glucose equivalents required to construct a leaf in terms of C skeletons, reductant, and ATP, excluding additional costs for maintenance and substrate transport (Williams *et al.*, 1989). Leaf CC_{mass} (g glucose g^{-1}) was estimated using the following equation (Vertregt & Penning de Vries, 1987; Poorter, 1994; Boyd *et al.*, 2009):

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

Eqn 3

(C_{mass}, leaf carbon concentration; Ash, leaf ash concentration (proxy for mineral concentration; Vertregt & Penning de Vries, 1987); N_{mass}, leaf N concentration (all in g g^{-1}).) We assumed leaf NO_3^- accumulation is negligible compared with organic N forms, and nitrate is the dominant form of N uptake. The first part of the CC equation above takes into account the C 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 the 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).

Metrics of leaf resource-use efficiencies

Resource-use efficiency (RUE) is broadly defined as the amount of C assimilated per unit resource (Funk & Vitousek, 2007). Potential photosynthetic energy-use efficiency (PEUE) was calculated as $A_{max,mass}/CC_{mass}$. Time-integrated PEUE was calculated as PEUE × LL, which accounts for the duration of potential returns on initial leaf investment. Potential photosynthetic N-use efficiency (PNUE) was calculated as $A_{max,mass}/$[leaf N]. For 17 species, time-integrated N-use efficiency (NUE) was calculated as $A_{max,mass}/$[leaf litter N] × LL (Table S1; see Aerts & Chapin, 1999; Hirose, 2012). As leaf N resorption data were not collected for all species, an additional time-integrated metric of PNUE was calculated as PNUE × LL ('lifespan PPNUE' *sensu* Reich *et al.*, 1992). The relationship between PNUE × LL (mol CO_2 g^{-1} leaf N) and NUE (mol CO_2 g^{-1} *unresorbed* N; incorporating N residence time) scaled in proportion with one another (i.e. isometric; Fig. S1). Therefore, we report our results using PNUE × LL as a robust estimate for time-integrated NUE, as this metric was calculated for the complete data set. In our data set, this tight relationship between metrics results from comparable rates of leaf N resorption between our study species ($P > 0.1$; Table S2). However, N resorption can differ between native and invasive species (I. Jo, unpublished data). These potential differences caution that PNUE × LL may not always be a reliable proxy for time-integrated NUE, as N mean residence times can be important in determining overall efficiency (Berendse & Aerts, 1987).

Daily C gain was estimated using the light response curves and daily PPFD measured at 30-min intervals from June to August (see Fridley, 2012), assuming the nighttime respiration rate to be 75% of the dark respiration rate measured during the day (Williams *et al.*, 1989). Payback time (days for net C gain to equal CC) was estimated as the ratio of CC to average daily C gain (Williams *et al.*, 1989) multiplied by log$_e$(2) to account for time-discounting effects (Poorter, 1994; Falster *et al.*, 2012). This estimation of payback time does not account for age-related

changes in photosynthesis or maintenance costs but can be considered a relative measure across species.

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 specific leaf area. All statistical analyses were performed in R (R Development Core Team, 2013). We analyzed univariate data with phylogenetic generalized least squares (PGLS) regression models, which accounted for relatedness in the data set through the phylogenetic distance matrix (see Fig. S2 for tree). We accounted for variation within species by weighting values by their intraspecific precision (standard error^{-1}). For each trait, we compared models with and without a fixed effect of native status (native or nonnative) using likelihood ratio tests, following a χ^2 distribution with one degree of freedom. Because the phylogeny was approximate and based on estimated branch lengths, we also performed an analogous analysis using linear mixed-effect models (Bates $et\ al.$, 2011) that accounted for intraspecific and genus-level variation through random effects. Results of this approach were qualitatively similar to PGLS and are excluded for brevity. When necessary, data were log-transformed to satisfy assumptions of variance homoscedasticity and normality of model residuals.

Bivariate trait relationships were analyzed with standardized major axis (SMA) line fitting implemented with the $smatr$ package in R (Warton $et\ al.$, 2012) using species means (see data Table S1). SMA line fitting minimizes residual variance in both x and y dimensions and is preferred in analyzing bivariate allometric relationships, as opposed to predicting y from x in classical regression (Warton $et\ al.$, 2006). Testing in the SMA routine involves first testing for common slopes between groups. If the slopes do not differ, the lines fitted to the groups may represent a shift along their common slope and/or shifts in elevation (y-intercept).

Lastly, we implemented principal components analysis (PCA) to understand, in a multivariate context, how leaf RUE metrics, C assimilation, and leaf longevity were related and if coordinated group variation separated native and invasive plants along axes of physiological functioning. We specifically chose these traits to include in the PCA to summarize the multivariate relationships of our hypothesis that focused on C- and N-use efficiency.

Results

Comparative functioning between native and invasive species

As a group, invaders had greater area-based net photosynthetic rates (A_{net}) than native species, at both saturating and relatively low PPFD (Fig. 1). However, area-based A_{net} was comparable between groups at and near 0 µmol photons $m^{-2}\ s^{-1}$ (Fig. 1; $R_{d,area}$, Table 2). Mass-based dark respiration ($R_{d,mass}$) was moderately greater in invasive species (Table 2). Photosynthetic differences were further reflected through greater maximum photosynthetic rates ($A_{max,area}$ and $A_{max,mass}$), maximum

carboxylation rates ($V_{c,max}$), and average area- and mass-based daily C gain (C gain$_{area}$ and C gain$_{mass}$) in invasive species (accounting for phylogenetic relatedness; Table 2). Respiration efficiency ($A_{max,area}/R_{d,area}$) was also slightly greater in invasive species, suggesting that respiratory costs were lower per unit photosynthetic gain than in native species.

Invasive species had significantly greater mean CC$_{area}$, N_{mass} and N_{area}, similar leaf C and Ash, and, subsequently, lower leaf C : N (Table 2). With higher values of both N_{area} and $A_{max,area}$, invasive species were shifted further along a shared tradeoff in the $A_{max,area}$–N_{area} relationship (Fig. 2a). Leaf N was more closely associated with $V_{c,max}$ than $A_{max,area}$, especially within invasive species (Fig. 2b). Among photosynthetic traits, the greatest correlation was between $A_{max,area}$ and $V_{c,max}$ (overall: $r^2 = 0.49$; $P < 0.001$), which describes the recognized relationship between the maximum carboxylase activity of Rubisco and the realized net C assimilation rate at ambient CO_2 concentrations. With significantly higher mean values in both traits (Table 2), invasive species were shifted further along a common slope (Fig. 2c).

Considering investments in tissue construction along with the subsequent duration of photosynthetic function, the relationship between daily C gain$_{mass}$ and LL was negative, although the correlation was weak (overall: $r^2 = 0.07$; $P = 0.15$). With both shorter LL and lower C assimilation among natives (Table 2), a significant elevation (y-intercept) shift in fitted SMA lines was detected ($P < 0.01$; Fig. 3a). Therefore, at a given LL, invaders had greater C gain$_{mass}$ (grouped in upper right of Fig. 3a). As expected, the payback time–LL relationship followed the inverse trend of daily C gain$_{mass}$–LL, with a positive, weak association (Fig. 3b). At a given LL, invaders tended to have shorter payback
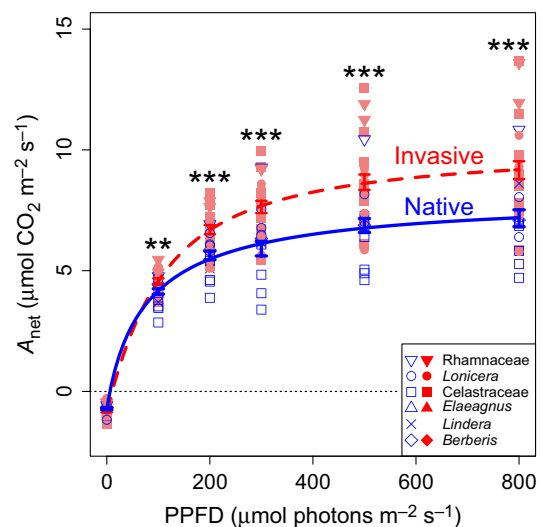

Fig. 1 Average modeled light response curves for 12 native (open symbols) and 18 invasive (closed symbols) species. Error bars (group mean ± 1 SE) show empirically measured peak season area-based net photosynthetic rates (A_{net}) at various irradiances (photosynthetic photon flux density (PPFD)). Statistical differences are between native and invasive groups evaluated from likelihood ratio tests of phylogenetic generalized least squares (PGLS) models (**, $P < 0.01$; ***, $P < 0.001$). Points indicate species means.

Table 2 Mean values ($\pm$ 1 SE) of photosynthetic, biochemical, structural, and resource-use efficiency leaf traits among native and invasive species

Trait (units) [a]	Invasive	Native	Native status (χ^2)
$A_{max,area}$ (μmol CO_2 m^{-2} s^{-1})	**11.19 $\pm$ 0.78**	8.10 $\pm$ 0.71	9.53**
$A_{max,mass}$ (μmol CO_2 g^{-1} s^{-1})	**0.2467 $\pm$ 0.0272**	0.1802 $\pm$ 0.0181	6.84**
$R_{d,area}$ (μmol CO_2 m^{-2} s^{-1})	0.79 $\pm$ 0.07	0.73 $\pm$ 0.06	2.04
$R_{d,mass}$ (μmol CO_2 g^{-1} s^{-1})	**0.0176 $\pm$ 0.0021**	0.0163 $\pm$ 0.0011	7.90**
A_{max}/R_d	**17.37 $\pm$ 2.06**	13.52 $\pm$ 1.64	6.09*
ϕ (μmol CO_2 μmol^{-1} photons)	0.076 $\pm$ 0.003	0.074 $\pm$ 0.003	2.35
LSP (μmol photons m^{-2} s^{-1})	370.5 $\pm$ 92.4	233.4 $\pm$ 55.2	<0.01
LCP (μmol photons m^{-2} s^{-1})	10.8 $\pm$ 1.0	9.7 $\pm$ 0.8	3.53
$V_{c,max}$ (μmol CO_2 m^{-2} s^{-1})	**46.10 $\pm$ 2.22**	32.24 $\pm$ 3.00	14.71***
Daily C gain$_{area}$ (mmol CO_2 m^{-2} d^{-1})	**273.8 $\pm$ 9.0**	223.9 $\pm$ 12.1	16.94***
Daily C gain$_{mass}$ (mmol CO_2 g^{-1} d^{-1})	**6.06 $\pm$ 0.53**	5.00 $\pm$ 0.40	10.15**
SLA (cm^2 g^{-1})	218.52 $\pm$ 12.75	233.42 $\pm$ 8.03	0.25
N_{mass} (%)	**2.97 $\pm$ 0.19**	2.52 $\pm$ 0.11	14.20***
N_{area} (g m^{-2})	**1.40 $\pm$ 0.08**	1.11 $\pm$ 0.06	15.57***
Ash (mg g^{-1})	91 $\pm$ 6	93 $\pm$ 8	4.22
C_{mass} (%)	45.00 $\pm$ 0.26	44.51 $\pm$ 0.40	1.46
C_{area} (g m^{-2})	22.37 $\pm$ 1.46	19.80 $\pm$ 0.71	3.44
C : N	16.54 $\pm$ 1.05	**18.60 $\pm$ 0.81**	6.51*
CC_{mass} (eq. g glucose g^{-1})	1.328 $\pm$ 0.018	1.384 $\pm$ 0.020	1.61
CC_{area} (eq. g glucose m^{-2})	**65.85 $\pm$ 4.16**	56.81 $\pm$ 2.28	6.13*
LL (d)	**145.1 $\pm$ 6.9**	120.9 $\pm$ 6.4	7.72**
PT (d)	6.12 $\pm$ 0.54	**7.25 $\pm$ 0.98**	6.95**
PNUE (μmol CO_2 g^{-1} N s^{-1})	8.28 $\pm$ 0.69	7.51 $\pm$ 0.67	3.57
PNUE $\times$ LL (mol CO_2 g^{-1} N)	**101.00 $\pm$ 8.61**	77.73 $\pm$ 8.20	8.52**
PEUE (μmol CO_2 kg^{-1} glucose s^{-1})	**183.44 $\pm$ 19.07**	137.95 $\pm$ 13.03	6.38*
PEUE $\times$ LL (kmol CO_2 kg^{-1} glucose)	**2.19 $\pm$ 0.19**	1.41 $\pm$ 0.13	15.29***

[a] $A_{max,area}$ and $A_{max,mass}$, area- and mass-based light-saturated gross photosynthetic rates on an area and mass basis, respectively ($A_{max,mass} = A_{max,area} \times$ SLA); $R_{d,area}$ and $R_{d,mass}$, area- and mass-based dark respiration rates at ambient [CO_2], respectively; A_{max}/R_d, respiration efficiency; ϕ, apparent quantum yield; LSP, 75% light saturation point; LCP, light compensation point; $V_{c,max}$, maximum carboxylation rate; daily C gain$_{area}$ and daily C gain$_{mass}$, area- and mass-based average daily carbon assimilation; SLA, specific leaf area; N_{mass} and N_{area}, mass- and area-based leaf nitrogen concentrations; Ash, leaf ash concentration; C_{mass} and C_{area}, mass- and area-based leaf carbon concentrations; CC_{mass} and CC_{area}, mass- and area-based leaf construction costs; LL, leaf longevity; PT, payback time, days to amortize leaf construction costs (Poorter, 1994); PNUE, photosynthetic nitrogen-use efficiency; PNUE $\times$ LL, 'life-span PPNUE' (*sensu* Reich *et al.*, 1992), an index of time-integrated PNUE; PEUE, photosynthetic energy-use efficiency; PEUE $\times$ LL, time-integrated PEUE.
The statistical significance of differences between native and invasive groups was determined using likelihood ratio tests (χ^2 with 1 df) that compared PGLS regression models for each trait with and without a fixed effect of native status. Significantly greater mean values are indicated in bold. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
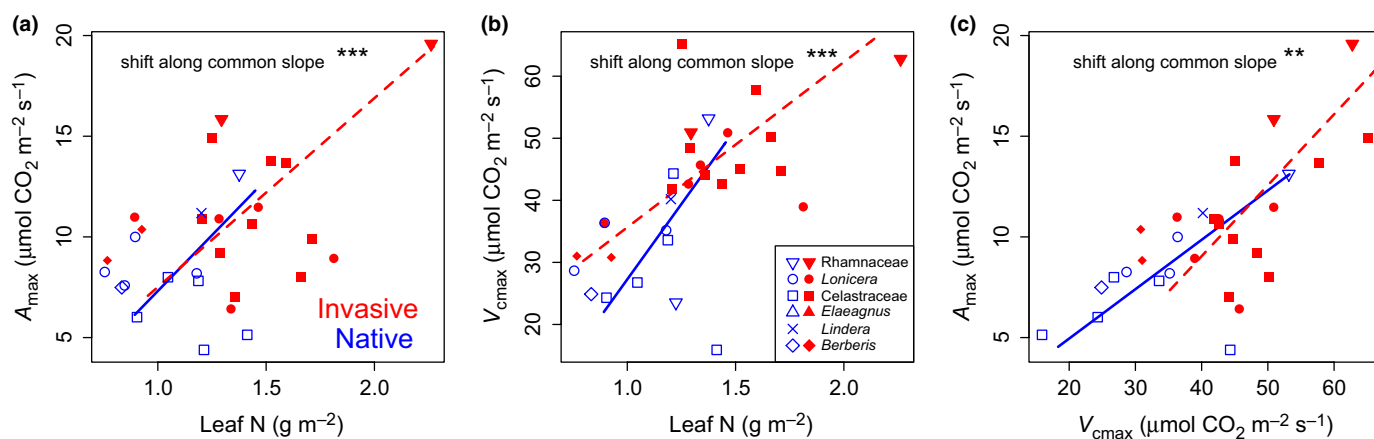
Fig. 2 Standardized major axis (SMA) relationships for maximum carbon (C) assimilation parameters and leaf nitrogen (N). Points indicate species means. (a) Light-saturated gross photosynthetic rate (A_{max})–N concentration (leaf N) (all species: $r^2 = 0.22$, $P < 0.01$; native: $r^2 = 0.01$, $P = 0.76$; invasive: $r^2 = 0.15$, $P = 0.12$), (b) maximum carboxylation rate ($V_{c,max}$)–leaf N (all species: $r^2 = 0.36$, $P < 0.001$; native: $r^2 = 0.07$, $P = 0.42$; invasive: $r^2 = 0.36$, $P < 0.01$), and (c) A_{max}–$V_{c,max}$ (all species: $r^2 = 0.49$, $P < 0.001$; native: $r^2 = 0.36$, $P < 0.05$; invasive: $r^2 = 0.38$, $P < 0.01$). Significance tests are from SMA for each relationship for differences in slope, elevation (y-intercept), and shift along the common fitted slope (**, $P < 0.01$; ***, $P < 0.001$).
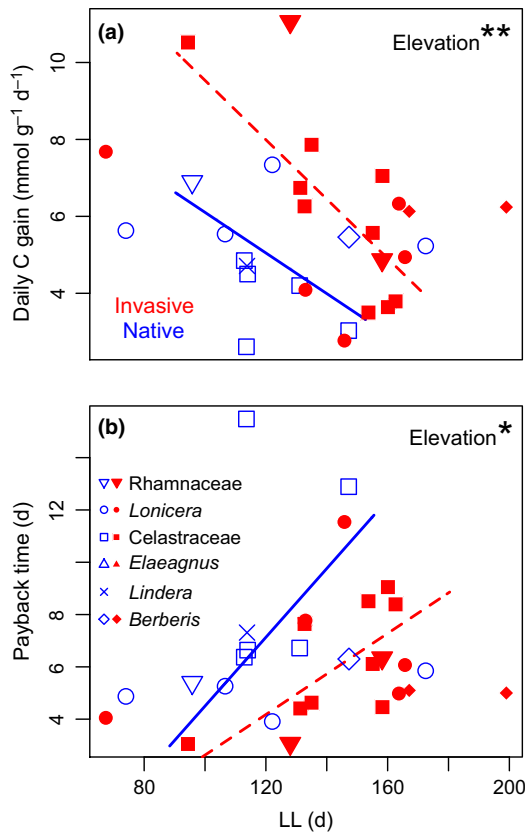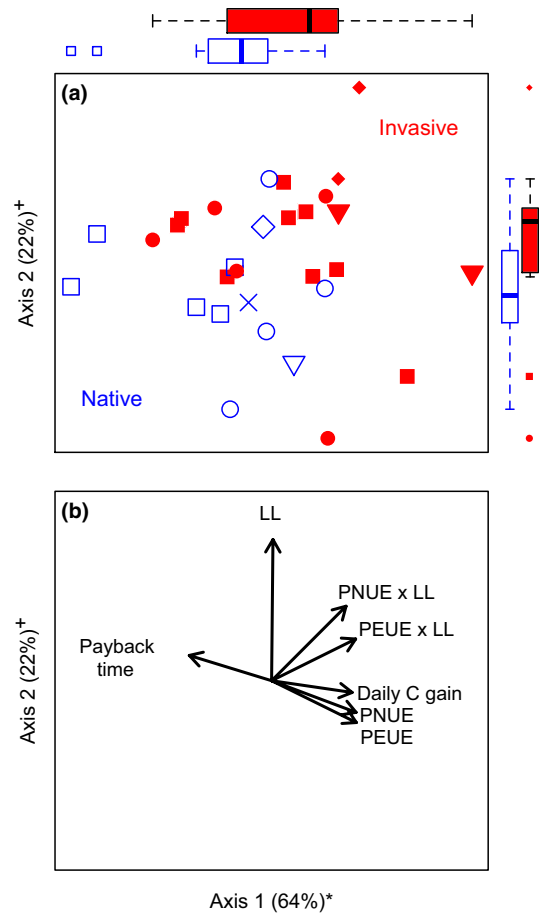
Fig. 3 Standardized major axis (SMA) relationships between (a) mass-based daily carbon gain (daily C gain$_{mass}$) and leaf longevity (LL) (all species: $r^2 = 0.07$, $P = 0.15$; native: $r^2 = 0.07$, $P = 0.41$; invasive: $r^2 = 0.24$, $P < 0.05$) and (b) payback time and LL (all species: $r^2 = 0.02$, $P = 0.46$; native: $r^2 = 0.04$, $P = 0.49$; invasive: $r^2 = 0.09$, $P = 0.23$). Points indicate species means. Significance tests are from SMA for each relationship for differences in slope, elevation (y-intercept), and shift along the common fitted slope (*, $P < 0.05$; **, $P < 0.01$).

Fig. 4 Ordination of native ($n = 12$; open symbols) and invasive ($n = 18$; closed symbols) species using principal components analysis (PCA) based on resource-use efficiency traits: payback time, leaf longevity (LL), indices of time-integrated photosynthetic nitrogen (N)-use efficiency (PNUE × LL) and energy-use efficiency (PEUE × LL), area-based daily C gain (Daily C Gain$_{area}$), PNUE, and PEUE. (a) Species scores along axes 1 and 2 and (b) trait loadings with vector length and direction corresponding to correlations between the trait and species scores. Axes 1 and 2 cumulatively explained 86% of the variance and separate native and invasive species' resource-use efficiency trait syndromes (two-tailed t-tests: +, $P < 0.1$; *, $P < 0.05$). Point symbols follow Fig. 3.

time (SMA elevation test; $P < 0.05$), even though invaders also had greater C costs in the form of glucose (CC$_{area}$) to compensate before achieving a net positive leaf C balance (Table 2).

Differences in instantaneous and time-integrated resource-use efficiencies

Although invaders exhibited both greater A_{max} and CC$_{area}$ than natives, mean PEUE ($A_{max,area}$/CC$_{area}$) differed between groups, indicating that invaders possessed greater instantaneous C returns per unit energy investment. As a consequence of greater LL in invasive species, especially at a given payback time (Fig. 3b), this difference in PEUE was magnified when integrated over time (PEUE × LL; Table 2). By contrast, differences were marginal in PNUE (Table 2; $P = 0.059$), which reflected a proportionately greater mean leaf N and $A_{max,area}$ among invasive species (Fig. 2a). However, because of substantially greater LL in invasive species (Table 2), marginal PNUE differences became significant when integrated over time (PNUE × LL). Conclusions remained the same when considering leaf N resorption rates in a species subset (see the Materials and Methods section; Fig. S1).

Multivariate trends in resource-use efficiencies

The first two axes of a PCA using RUE traits explained 86% of the variation in the data set, and separated native and invasive species (Fig. 4a; two-sided t-tests of species' axis scores by native status: axis 1: $t = -2.25$, df $= 28$, $P = 0.03$; axis 2: $t = 1.89$, df $= 28$, $P = 0.07$). Axis 1 (64% of variance explained) was positively correlated with area-based daily C gain (daily C gain$_{area}$), PEUE, and PNUE, and negatively correlated with payback time, which matches univariate and bivariate testing (Table 2; Fig. 3). Axis 2 (22% of variance explained) was most strongly positively correlated with LL (Fig. 4b). LL was orthogonal to daily C gain$_{area}$, which echoes the bivariate tests that indicated that commonly held physiological tradeoffs involving LL were less constraining to productivity in invasive species relative to natives (Fig. 2).

Discussion

Do invasive species follow different resource-use strategies?

Much of our current mechanistic understanding of plant invasions stems from studies in anthropogenic, disturbed habitats of high fertility (Martin *et al.*, 2009), which show that invaders often exhibit greater resource acquisition rates, not necessarily differences in RUE or different constraints in leaf function (e.g. Leishman *et al.*, 2010; Ordonez & Olff, 2013). In other words, native and invasive plants in a given community may follow the same general set of resource capture strategies and trait tradeoffs that have been generalized for species globally (e.g. Reich *et al.*, 1997; Wright *et al.*, 2004, 2005). We tested this premise in species common to ENA deciduous forest understories to investigate whether congeneric invasive and native species are similarly constrained to a common set of tradeoffs, or alternatively, whether species invasive in ENA exhibit more efficient resource-use strategies, suggesting greater C gain per unit resource invested. Among 32 native and invasive species common to ENA forests, we found evidence that invaders are both more productive and more efficient—they exhibit greater daily C gain and also greater C gain per unit C or N invested in leaf tissue relative to their native competitors (Table 2). Expanding upon past invasion studies (e.g. Baruch & Goldstein, 1999; Funk & Vitousek, 2007; Boyd *et al.*, 2009; Leishman *et al.*, 2010), these differences were most pronounced when integrated over time.

Invaders as a group exhibited significantly longer LL and greater CC_{area} – traits associated with high resource conservation, low growth rate, and lower competitive ability (Aerts & Chapin, 1999; Westoby *et al.*, 2002; Wright *et al.*, 2004). This finding of longer LL for invasive species builds upon the surprising recent finding that ENA forest invaders have greater relative C gains into the autumn, utilizing a temporal niche absent in the native flora (Fridley, 2012). Plants adapted to low-resource environments are expected to exhibit conservative resource-use strategies, but at the expense of fast growth (Aerts & Chapin, 1999). In low-resource ecosystems, the success of invasive species may therefore depend on greater resource conservation than native species, but with proportionately slower absolute growth rates. In ENA forests, we found that invaders had greater RUEs and similar light-use efficiencies compared with native species. Surprisingly, in addition to more conservative resource-use traits, invaders also exhibited traits associated with greater productivity. With both greater photosynthetic gains (Fig. 1) and greater mean LL, invaders as a group exhibited greater energy-use and N-use efficiencies through time (PEUE × LL; Table 2). LL was weakly related to photosynthetic functioning (Fig. 3) and separated invaders on an axis orthogonal to C gains (Fig. 4), which suggests that tradeoffs between resource investments and C returns are distinct between native and invasive species in ENA. Therefore, compared with native species, resource-use strategies of invasive species were not only more efficient but also more productive.

Past studies have found RUE differences between native and invasive species across a range of habitats (e.g. McDowell, 2002;

Nagel & Griffin, 2004; Funk & Vitousek, 2007; Osunkoya *et al.*, 2010), including in an ENA forest (Boyd *et al.*, 2009). Funk & Vitousek (2007) found greater instantaneous PEUE and PNUE in invaders in Hawaii across light- and N-limited habitats. However, they found that natives had comparable RUEs when integrated over the lifespan of the leaf. In light of instantaneous differences and time-integrated similarities in RUEs, they reasoned that invasion was driven by dynamics on short (seasonal) timescales. We observed a different pattern in ENA temperate forests, which could be attributable to the deciduous environment and potential fitness advantages of extended leaf phenology (Fridley, 2012). In ENA, invasion could be explained by later autumn senescence among invasive species (Fridley, 2012) and longer LL that was largely independent of daily C gain$_{area}$ (Fig. 3).

Other studies have stressed similarities in leaf resource economics among native and invasive plants (e.g. Leishman *et al.*, 2007, 2010; Ordonez *et al.*, 2010; Peñuelas *et al.*, 2010; Ordonez & Olff, 2013). In a recent study comparing natives and invaders in Australia, Leishman *et al.* (2010) concluded that species from both groups followed metabolic tradeoffs consistent with leaf economics theory. Comparing the slopes of leaf trait relationships for native and invasive plants, they found that, across many trait relationships, natives had strategies at the slow returns end of a common, coordinated axis of plant strategies, with lower C assimilation rates proportionate with lower resource needs. Similarly, in ENA understory species, we found group shifts along common slopes for instantaneous photosynthesis- and N-related traits (Fig. 2). However, when considering other traits (e.g. CC_{area} and LL), our results suggest that ENA invaders are both more productive and more efficient than natives (Table 2; Figs 3, 4). Unlike Leishman *et al.* (2007, 2010), we found greater RUEs among invasive species. Because RUE is a ratio, differences can be found along a common slope in a bivariate relationship, suggesting that an RUE difference alone is not sufficient to conclude a fundamental difference in resource capture strategies (defined as differences in bivariate slope relationships; Leishman *et al.*, 2010). Although N-related functional relationships in this study shared slopes between groups (Fig. 2), we found invaders to be more resource-use efficient as a product of greater cumulative C gains per unit invested, which is indicative of different physiological constraints between native and invasive species.

Our conclusions indicating resource-use strategy differences between native and invasive plants contrast with conclusions of these past studies for two possible reasons. First, many studies focused on instantaneous measures and did not incorporate temporal traits. Therefore, we cannot directly compare our results with those of past studies that do not consider LL. Although perhaps less important in disturbed ecosystems, the integration of time into functional comparisons plays a critical role when leaf duration ultimately determines whole-plant cumulative C gain (Reich *et al.*, 1992; Westoby *et al.*, 2002), especially in light- and N-limited ENA forests (Aber *et al.*, 1993; Finzi & Canham, 2000). Additionally, the conclusions of Leishman *et al.* (2010) may be more representative of invasions in disturbed, fertile habitats, as few invasive species were found in undisturbed habitats in

their study. However, Ordonez & Olff (2013) considered trait differences across resource and disturbance gradients and found that, compared with natives, invasive species in high-resource environments had greater mean trait values associated with fast growth, but trait differences between groups were similar across environments. Because individuals in our study were grown in a common environment, we tested inherent physiological differences, rather than *in situ* performance in different habitats.

Unexpectedly, we found that ENA invaders had significantly greater CC$_{area}$ and, although not significant, lower mean specific leaf area (Table 2). Low CC has been invoked as a primary measure of invasion potential (Nagel & Griffin, 2001). However, studies have reported mixed results and interpretations, including invasive species with lower CC (Baruch & Goldstein, 1999; Nagel & Griffin, 2001; Boyd *et al.*, 2009; Osunkoya *et al.*, 2010) and greater CC (McDowell, 2002). Patterns in leaf CC alone may be insufficient to understand invasions across habitats, because invested costs are without ecological context unless viewed in light of C returns (Griffin, 1994). Williams *et al.* (1989) proposed payback time (days to amortize CC) as a trait to explain ecological variation in LL across habitats. Our measure of payback time can be considered a relative estimate across species because we did not directly account for leaf age-related declines in photosynthetic rates. In our data, the payback time–LL relationship was weak, although natives and invaders clearly occupied different portions of trait space (Fig. 3b). Further, at a given LL, invasive species tended to have greater C returns than natives (elevation shift; Fig. 3b). Because plants should be expected to retain leaves longer than their payback time to achieve a net positive C balance (Westoby *et al.*, 2002; Falster *et al.*, 2012), it is reasonable to expect the LL–payback time relationship to be weak within deciduous species. However, all else being equal, the tradeoff between LL and daily C gain among co-occurring plants should be expected to equalize fitness and maintain strategies along that continuum (Falster *et al.*, 2012). Tradeoffs with LL were weak in our data, with ENA invaders achieving greater C gains (Figs 1, 2), a greater C assimilation rate at a given LL (Fig. 3a), and greater PEUE through time (Table 2).

Why are East Asian invaders less constrained by metabolic tradeoffs than ENA natives?

ENA invaders appear to be less constrained in their allocation to rapid growth versus long-lived tissues than the native flora, yet it remains unclear why native species would not also exhibit such strategies. One possibility is that we did not measure an important trait that, if measured or integrated over the whole plant, would equalize our reported differences in leaf resource economics. For instance, greater herbivore pressure in natives could lead to lower competitive performance (e.g. Keane & Crawley, 2002), thereby explaining why invasive plants in our study have longer LL without paying the expected metabolic costs. However, given that invasion between the Eurasian and ENA forest ecosystems is asymmetric, with East Asia contributing more invaders to ENA (Fridley, 2008) than vice versa (Weber *et al.*, 2008), scenarios that invoke home range herbivory alone are unlikely to be general

for this group of invasive species. Also, East Asian species co-evolved with earthworms, which were largely absent from ENA until recent human introductions (Nuzzo *et al.*, 2009). Therefore, the strategies of East Asian species may be better adapted than ENA natives to soil conditions maintained by earthworms, such as increased N cycling. It is uncertain if East Asian species evolved under lower soil nutrient availability to promote increased RUE. However, we found increased C gains for invasive species in addition to greater RUEs, which cannot be explained by historically different soil nutrient conditions alone.

Although tradeoffs in leaf functional traits are broadly consistent world-wide (e.g. Wright *et al.*, 2004), there may be important differences in plant functional strategies between regions as a result of historical constraints (Heberling & Fridley, 2012). Fourteen of the 18 species measured in the current study have native distributions that include East Asia (Table 1). Despite both regions lying primarily in the temperate deciduous forest biome and composed of closely related taxa that diverged in the late Miocene (Donoghue & Smith, 2004), the flora of East Asia has experienced very different environmental conditions over the past several millennia, resulting in higher species diversity, endemism, and phylogenetic diversity (Qian & Ricklefs, 2000). Community-level properties, such as competitive pressure, disturbance, and time for resident species to adapt and fill niches, may make some communities more or less vulnerable to invasion ('community maturity' *sensu* Shea & Chesson, 2002). From this regional perspective, we speculate that invasive plants introduced from East Asia may have 'pre-adapted' traits in the native range that confer invasiveness in ENA (Fridley, 2011). However, ecophysiological comparisons in the home range would be needed to confirm this hypothesis.

Conclusions

We found both higher productivity and more efficient resource use in forest understory invaders in ENA compared with their native congeners, and lower metabolic constraints between LL and C gain in invaders. From a leaf-level perspective, we found invaders' competitive success to probably be attributable to greater C gains, and, despite greater leaf N and energy resource investments, a greater duration of returns. This conclusion supports past findings emphasizing the importance of RUE in invasions in resource-limited ecosystems (Funk & Vitousek, 2007) and, in ENA forests, the functional importance of leaf phenology differences in the invasive flora (Fridley, 2012). If these findings are general, then such differences in the leaf function of invaders may be expected to drive large shifts in the productive capacities and nutrient budgets of deciduous forest ecosystems.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Isometric relationship between time-integrated nitrogen-use efficiency measures in a species subset.

Fig. S2 Phylogeny of the studied species.

Table S1 Summary of leaf trait data for each species

Table S2 Summary statistics for additional nitrogen-related variables in a species subset

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