LETTER

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Extended leaf phenology and the autumn niche in deciduous forest invasions

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The phenology of growth in temperate deciduous forests, including the timing of leaf emergence and senescence, has strong control over ecosystem properties such as productivity[1,2] and nutrient cycling[3,4], and has an important role in the carbon economy of understory plants[5–7]. Extended leaf phenology, whereby understory species assimilate carbon in early spring before canopy closure or in late autumn after canopy fall, has been identified as a key feature of many forest species invasions[5,8–10], but it remains unclear whether there are systematic differences in the growth phenology of native and invasive forest species[11] or whether invaders are more responsive to warming trends that have lengthened the duration of spring or autumn growth[12]. Here, in a 3-year monitoring study of 43 native and 30 non-native shrub and liana species common to deciduous forests in the eastern United States, I show that extended autumn leaf phenology is a common attribute of eastern US forest invasions, where non-native species are extending the autumn growing season by an average of 4 weeks compared with natives. In contrast, there was no consistent evidence that non-natives as a group show earlier spring growth phenology, and non-natives were not better able to track interannual variation in spring temperatures. Seasonal leaf production and photosynthetic data suggest that most non-native species capture a significant proportion of their annual carbon assimilate after canopy leaf fall, a behaviour that was virtually absent in natives and consistent across five phylogenetic groups. Pronounced differences in how native and non-native understory species use pre- and post-canopy environments suggest eastern US invaders are driving a seasonal redistribution of forest productivity that may rival climate change in its impact on forest processes.

Phenological studies of understory leaf display and gas exchange for native woody species in eastern US (EUS) forests demonstrate a critical period of carbon gain in spring before canopy closure[6,7,13,14]. Significant carbon gain after canopy leaf fall, however, seems to be rare for native forest shrubs[13,14], presumably because lower autumnal solar radiation means deciduous species have less to gain by delaying senescence[1,6]. On the other hand, comparative studies of co-occurring native and non-native understory species[5,8,9] have demonstrated both earlier and later carbon gain for non-natives, suggesting that extended leaf phenology could be an important mechanism of invader establishment in EUS forests[12,15]. To determine whether this pattern is general across a broad taxonomic sample of native and non-native species, I established an experimental garden of three replicate blocks of 73 woody species common to EUS deciduous forests, including native and non-native representatives of several phylogenetic groups (*Celastrus*, *Euonymus* in Celastraceae; *Elaeagnus* in Elaeagnaceae; *Frangula*, *Rhamnus* in Rhamnaceae; *Lonicera* in Caprifoliaceae; *Viburnum* in Adoxaceae) and other unrelated but widespread natives (Supplementary Table 1). All 30 non-native species are naturalized in the EUS and all but eight are currently managed as forest invaders[16]. From the onset of local forest canopy closure (approximately 20 May) until canopy leaf fall (approximately 24 Oct), plants were grown under 80% shade to simulate a deciduous understory light environment. For three growing seasons (2008–2010), we monitored the timing of spring foliar bud and leaf development, biweekly leaf production and chlorophyll (Chl) content, and monthly photosynthetic rate on select leaves at a range of light levels (50–800 $\mu mol\, pm^{-2}\, s^{-1}$). Although not all species were measured each year, a similar number of native and non-native species were monitored annually and data sets for most species involved at least 2 years (Supplementary Table 1).

The timing of leaf emergence across species was sensitive to interannual variation in spring temperatures (Supplementary Fig. 1), with all stages of bud development occurring several weeks earlier in the warmer spring of 2010 ($P < 0.001$, year contrasts in Mann–Whitney *U*-tests adjusted for multiple testing; Fig. 1). However, the timing of early stages of bud activity was not significantly different between native and non-native species for any year (Fig. 1). As a group, non-native species showed earlier budburst in 2010 and earlier full extension of true leaves in 2008 and 2010, but differences in median date were small (3, 1 and 2 days, respectively) and there was no evidence that non-natives were more responsive to the warmer spring of 2010 (year–nativity interaction, $P > 0.5$). In contrast, the timing of autumn leaf fall for non-native species as a group was delayed by as much as 28 days compared with natives (Fig. 1). The median date of 50% leaf fall for native species across 2008–2010 was 16 September, and for non-native species 13 October; the same comparison for 90% leaf fall was 27 October and 9 November. Autumn leaf phenology did not vary significantly across years (Akaike information criterion of models with and without year random effect, 2,512 versus 2,495, $P < 0.001$, likelihood ratio = 15.58 on 1 d.f.). Owing to the large difference in autumn phenology, non-native species on average had a growing season 29 days longer than natives, using days of extant true leaves until 50% leaf fall, which amounts to an extension over the native growing season of 19%.

Leaf Chl and gas exchange measurements supported strong maintenance of leaf function for non-native species after leaves of most natives had senesced. Non-native species retained high levels of leaf Chl in autumn compared with native species, despite similar spring Chl phenology (Fig. 2). In spring and summer, Chl content of both groups was determined by whether leaves were produced in sun or shade, with sun leaves peaking in Chl content in mid-August, 16 days before shade leaves ($P < 0.001$, $t = -3.76$ on 510 d.f.). In contrast, Chl content was identical for sun and shade leaves after mid September within both non-native and native groups, but non-native species showed significant delays in Chl breakdown, with an average difference in the date of 50% peak Chl loss between natives and non-natives of more than 2 weeks (Fig. 2; $P < 0.001$, $t = -3.54$ on 83 d.f.). Photosynthetic rates for both high (800 photosynthetic photon flux density (PPFD)) and low (100 PPFD) light levels followed the seasonal trajectory of Chl content for both native and non-native species, with peaks in summer, relatively high rates in spring, and no differences between groups (Supplementary Fig. 2). In autumn, photosynthetic rates for most native species (30 out of 43 species) declined to zero because of loss of live leaves, whereas most non-native species (21 out of 30 species) continued to assimilate carbon. Of the subset of natives and non-natives with live leaves after shade cloth removal, non-natives

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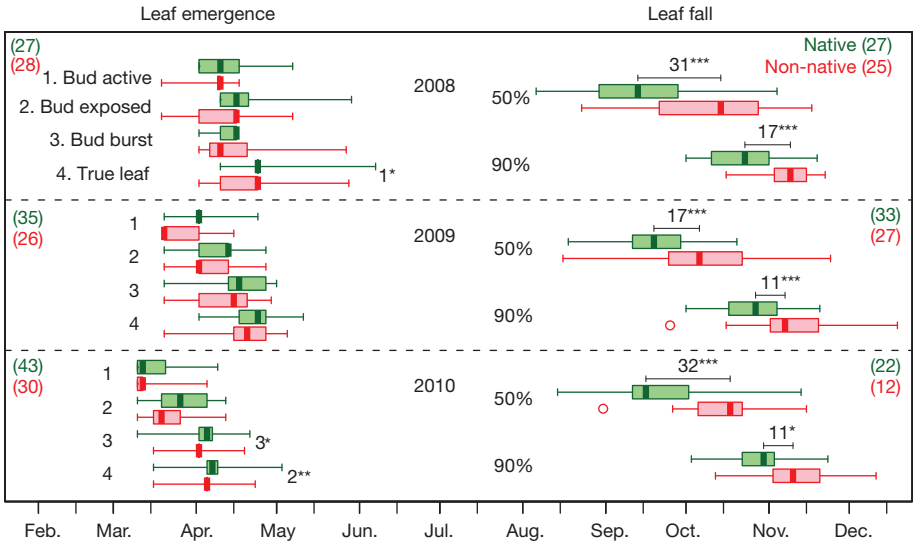

Figure 1 | Seasonal patterns of leaf emergence and leaf fall for native and non-native species over three growing seasons. Boxplots show data range with boxed first and third quartiles, median as heavy line, and point outliers; numbers of species for each group are indicated. Leaf emergence was monitored at 2- to 5-day intervals using a classification of budbreak stages and dates at which 50% and 90% of total leaves had fallen were interpolated from biweekly monitoring. Values indicate median difference in days between natives (green) and non-natives (red). *P* values are from Mann–Whitney *U*-tests adjusted for multiple testing (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

had marginally significant higher rates of photosynthesis in high light (Supplementary Fig. 2).

To quantify the impact of extended growth phenology on the total annual carbon (C) gain of native and non-native species, I estimated daily C assimilation for each species with a stochastic simulation model using empirical distributions of seasonal leaf production and photosynthetic capacity (see Methods). Most species captured a significant portion of their annual C assimilate before canopy closure on 20 May (Fig. 3a), with two-thirds of the species getting at least 10% of their annual C in the spring (mean = 14%). Natives as a group had a larger contribution of pre-canopy C gain than non-natives, both overall ($P < 0.05$, $t = 2.06$ on 70 d.f.) and after accounting for phylogenetic groups with a random effect ($P < 0.05$, $F = 4.22$ on 1, 63 d.f.), although separate tests within groups were not significant (Fig. 3b). Of those species of highest spring C gain, only one non-native species (*Lonicera* × *bella*) made the top 10 and only four made the top 20. In contrast, post-canopy C assimilation (after 24 October) was strongly biased towards non-native species and virtually absent in natives, with only three native species (*Diervilla rivularis*, *Diervilla lonicera*, *Lonicera sempervirens*) gaining more than 10% of their annual C in autumn, and more than half of the natives (25 out of 43 species) obtaining less than 1% (Fig. 3c). Nearly half of the non-native species (13 out of 30 species) obtained at least 5% of their C in autumn, and seven gained more than 10%, up to a maximum of 21% (*Lonicera fragrantissima*). The strong non-native C gain advantage in autumn was highly significant when controlling for phylogenetic group as a

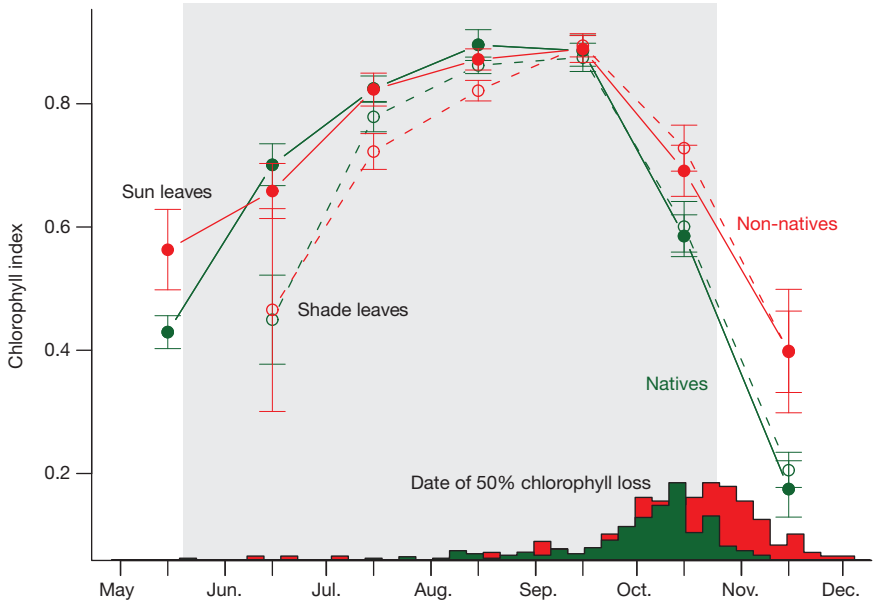

Figure 2 | Relative leaf Chl content for native and non-native species. Mean (± s.e.m.) content for native (green) and non-native (red) species are grouped by whether leaves were produced before (filled circles and lines) or after (open circles and dashed lines) canopy shading (grey region). Histograms show distributions of the date of 50% Chl loss, relative to peak Chl reading per leaf, for native ($n = 354$ leaves) and non-native species ($n = 253$) pooled across 2009 and 2010 growing seasons.

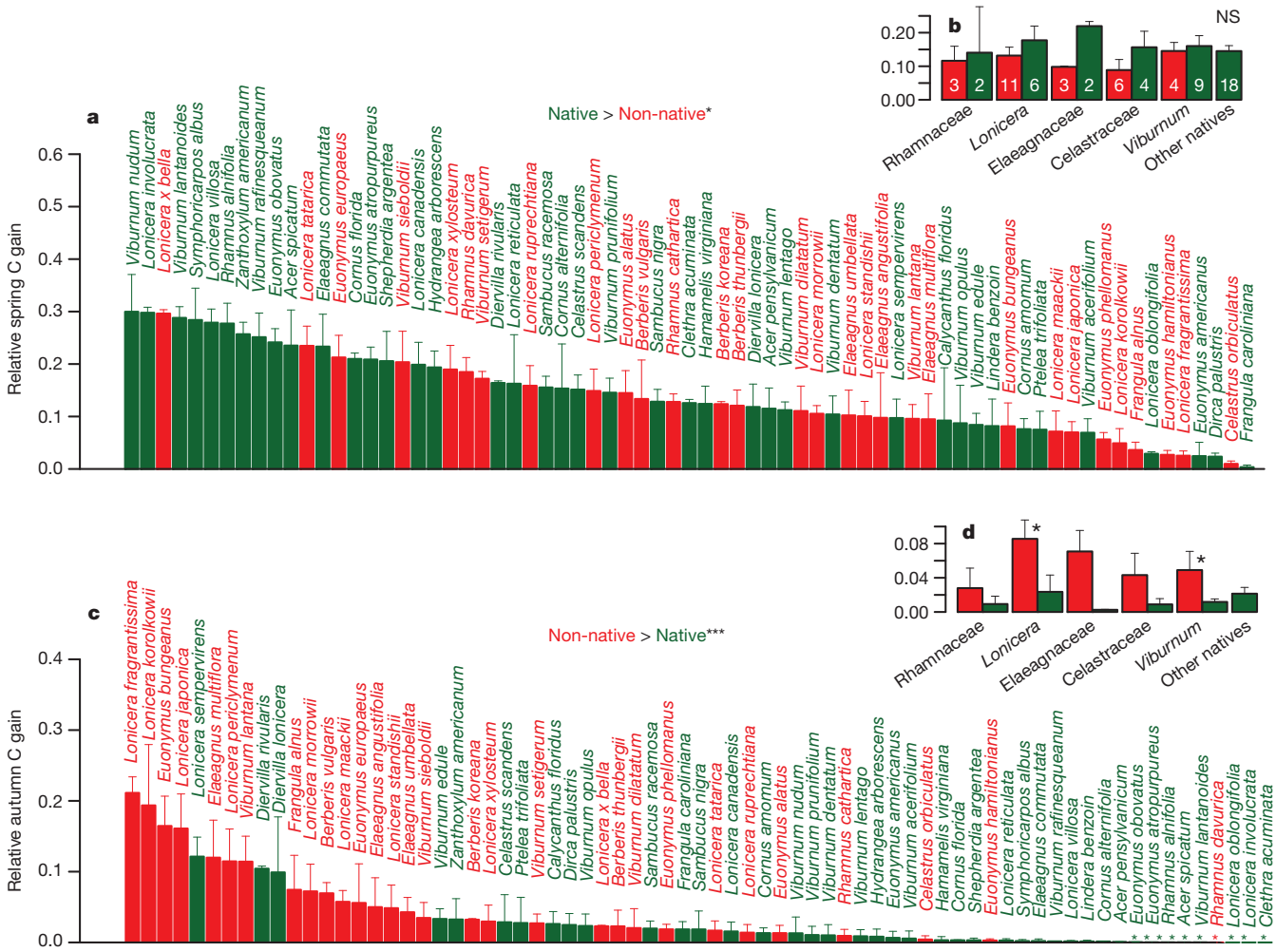

Figure 3 | Proportion of total annual C assimilated in spring and autumn for native and non-native species. Values of assimilation before (**a**, **b**) and after (**c**, **d**) shade cloth placement for native (green) and non-native (red) species were estimated by stochastic simulation of daily leaf area, light levels and photosynthetic capacity using empirical measurements (2008–2010). Values are means (± s.e.m.) of 1,000 permutations incorporating measured variation in individual and interannual leaf production and photosynthetic light curves. Inset figures (**b**, **d**) show mean (± s.e.m.) species values summarized by phylogenetic group, with sample sizes indicated. Black asterisks indicate statistical significance for overall native–non-native comparisons and Mann–Whitney *U*-tests within groups (*$P < 0.05$, ***$P < 0.001$). Coloured asterisks denote autumn C gain less than 0.5%. NS, not significant.

random effect ($P < 0.001$, $F = 15.81$ on 1, 63 d.f.), although small sample sizes within groups other than *Lonicera* and *Viburnum* precluded detection of significant nativity trends when groups were analysed separately (Fig. 3d).

Although non-native species seem to inhabit an autumn niche that is rare in the native woody flora, it is not clear from these data whether this constitutes their primary fitness advantage over natives. Across all species, total annual C gain was significantly associated with both early and late growth phenology ($P < 0.05$, $F = 5.28$ and 11.14 on 1, 59 d.f. for spring and autumn relative C gain, respectively, including a random phylogenetic group effect), confirming that earlier budbreak and delayed leaf senescence behaviours contribute to annual growth rates. However, non-native species overall did not assimilate more C annually than natives ($P > 0.3$, $F = 0.86$ on 1, 63 d.f.), partly because of the significant spring advantage of natives. Because spring phenology was variable but autumn phenology was not, the relative contribution of extended autumn phenology to the success of invaders may depend on spring temperatures, and it is possible that earlier springs will favour native species. This analysis does not include seasonal C losses from night-time respiration, however, which for many deciduous species are highest in spring[13].

The presumed costs of late leaf display for winter deciduous species are nutrient loss from lack of resorption in frost-damaged leaves[17] and shoot damage from delayed tissue hardening[18]. Why should colonizing deciduous species from temperate Eurasian environments not bear these costs? One possibility is that non-natives are better adapted to the warmer autumn temperatures experienced in the EUS over the past several decades[19], or are more responsive to elevated levels of soil nitrogen availability from industrial pollution[20], reducing their need to maximize resorption. Recent environmental changes cannot be a general explanation, however, given that many of the non-native species in the present study have been invasive for over a century[21]. On the other hand, increased soil nutrient fluxes in North American forests from Eurasian earthworm invasion may have been coincident with plant introductions[22]; it is conceivable that non-native species, having co-evolved with earthworms, evolved a nutrient-use strategy that is less dependent on autumn resorption, thus explaining observed associations of invasive shrub and earthworm abundance[23]. It is also notable that most of the invasive shrubs and lianas in EUS are from East Asia[16], a region that experienced significantly less climate disruption than EUS during the Pleistocene[24]. It is possible that the more restricted growth phenology of the EUS flora today is a relictual behaviour from shorter Pleistocene growing seasons[25], leaving some East Asian species 'pre-adapted' to the modern EUS forest environment[26]. However, the extended growth phenology of several species from Europe, a region of more severe Pleistocene climate disruption than EUS, would still require explanation.

Although it is not possible from this study to quantify the ecosystem impacts of extended foliar phenology of understory non-native species under natural forest conditions, eddy flux data[1,27,28] indicate that even minor changes in growing season duration can have a significant effect on forest productivity. In this context the impacts of forest invaders extending the period of C assimilation into autumn by several weeks may rival that of climate forcing[1], although additional studies of net C balance are needed to quantify potential differences in the seasonal C contribution of native and non-native species[28]. The higher autumnal activity of invaders may also lead to significant shifts in nutrient cycling, particularly if leaf nitrogen resorption is reduced in non-natives as a result of delayed senescence, causing significant changes in forest-floor litter quality[29]. Although their contribution to forest standing biomass is small, understory species can have disproportionate impacts on ecosystem fluxes[3,30], which suggests the extended understory growing season in deciduous forests resulting from continuing invasions by non-native shrubs, lianas and some herbs[10] may be a major driver of anthropogenic ecosystem change in eastern North America.

METHODS SUMMARY

The garden was established in 2006–2007 in Syracuse, New York, USA (43° 03′ N, 76° 09′ W). It included genera for which there exist at least one native species and one non-native invasive species present in EUS forests (see ref. 16 for details on 'non-native', 'invasive' and habitat criteria), in addition to 16 widespread but unrelated native species (Supplementary Table 1). Transplants were collected from the wild in central New York where possible (20 native and 9 alien species); those absent from wildlands in the region were obtained from commercial growers of similar latitude (Supplementary Table 1). Plants were spaced 1 m apart in three replicate blocks and covered with 80% knitted black shade cloth from 20 May to 24 October each monitoring year (2008–2010). We monitored spring bud and leaf development on each plant by photographing select nodes at 2- to 5-day intervals from early March to mid-May and classifying images according to five development stages. Leaf demography and Chl content (CCM-200 sensor) were monitored at 2-week intervals on five branches selected at random per individual per year. Photosynthesis was monitored monthly for each individual at intensities of 800, 300, 100 and 50 μmol photon $m^{-2} s^{-1}$ (LI-COR 6400; 400 μmol CO_2 mol^{-1}, 700 μmol s^{-1} flow rate, 20 °C). Fitted parameters for the non-rectangular hyperbolic light curve function (apparent quantum yield (AQY), A_m, R_d, α) were used in seasonal C gain simulations, incorporating daily leaf area from leaf demography data and daily light levels from a photosynthetically active radiation sensor. C gain summaries were derived from 1,000 annual permutations; for each, photosynthetic parameters were randomly sampled from species- and season-specific normal distributions and daily leaf area was determined by random samples from empirical distributions of daily leaf counts.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. Richardson, A. D. *et al.* Influence of spring and autumn phenological transitions on forest ecosystem productivity. *Phil. Trans. R. Soc. B* **365,** 3227–3246 (2010).
2. Polgar, C. A. & Primack, R. B. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytol.* **191,** 926–941 (2011).
3. Muller, R. N. & Bormann, F. H. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. *Science* **193,** 1126–1128 (1976).
4. Ehrenfeld, J. G. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6,** 503–523 (2003).
5. Harrington, R. A., Brown, B. J. & Reich, P. B. Ecophysiology of exotic and native shrubs in southern Wisconsin. I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* **80,** 356–367 (1989).
6. Augsperger, C. K., Chesseman, J. M. & Salk, C. F. Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. *Funct. Ecol.* **19,** 537–546 (2005).
7. Rothstein, D. E. & Zak, D. R. Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. *Funct. Ecol.* **15,** 722–731 (2001).
8. Schierenbeck, K. A. & Marshall, J. D. Seasonal and diurnal patterns of photosynthetic gas exchange for *Lonicera sempervirens* and *L. japonica* (Caprifoliaceae). *Am. J. Bot.* **80,** 1292–1299 (1993).
9. Xu, C.-Y., Griffin, K. L. & Schuster, W. S. F. Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. *Oecologia* **154,** 11–21 (2007).
10. Myers, C. V. & Anderson, R. C. Seasonal variation in photosynthetic rates influences success of an invasive plant, garlic mustard (*Alliaria petiolata*). *Am. Midl. Nat.* **150,** 231–245 (2003).
11. Wolkovitch, E. M. & Cleland, E. E. The phenology of plant invasions: a community ecology perspective. *Front. Ecol. Environ* **9,** 287–294 (2011).
12. Willis, C. G., Ruhfel, B. R., Primack, R. B., Miller-Rushing, A. J. & Losos, J. B. Favorable climate change response explains non-native species' success in Thoreau's Woods. *PLoS ONE* **5,** e8878 (2010).
13. Gill, D. S., Amthor, J. S. & Bormann, F. H. Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. *Tree Physiol.* **18,** 281–289 (1998).
14. Augsperger, C. K. & Bartlett, E. A. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiol.* **23,** 517–525 (2003).
15. Webster, C. R., Jenkins, M. A. & Jose, S. Woody invaders and the challenges they pose to forest ecosystems in the Eastern United States. *J. For.* **104,** 366–374 (2006).
16. Fridley, J. D. Of Asian forests and European fields: Eastern U.S. plant invasions in a global floristic context. *PLoS ONE* **3,** e3630 (2008).
17. May, J. D. & Killingbeck, K. T. Effects of preventing nutrient resorption on plant fitness and foliar nutrient dynamics. *Ecology* **73,** 1868–1878 (1992).
18. Saxe, H., Cannell, G. R., Johnsen, Ø., Ryan, M. G. & Vourlitis, G. Tree and forest functioning in response to global warming. *New Phytol.* **149,** 369–400 (2001).
19. Mitchell, T. D. & Jones, P. D. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* **25,** 693–712 (2005).
20. Aber, J. D., Nadelhoffer, K. J., Steudler, P. & Melillo, J. M. Nitrogen saturation in northern forest ecosystems. *Bioscience* **39,** 378–387 (1989).
21. Mack, R. N. Plant naturalizations and invasions in the Eastern United States: 1634–1860. *Ann. Mo. Bot. Gard.* **90,** 77–90 (2003).
22. Frelich, L. E. *et al.* Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biol. Invasions* **8,** 1235–1245 (2006).
23. Nuzzo, V. A., Maerz, J. C. & Blossey, B. Earthworm invasion as the driving force behind plant invasion and community change in Northeastern North American forests. *Conserv. Biol.* **23,** 966–974 (2009).
24. Ehlers, J. & Gibbard, P. L. The extent and chronology of Cenozoic global glaciation. *Quat. Int.* **164,** 6–20 (2007).
25. Lechowicz, M. J. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *Am. Nat.* **124,** 821–842 (1984).
26. Mack, R. N. Phylogenetic constraint, absent life forms, and preadapted alien plants: a prescription for biological invasions. *Int. J. Plant Sci.* **164,** S185–S196 (2003).
27. Goulden, M. L., Munger, J. W., Fan, S.-M., Daube, B. C. & Wofsy, S. C. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271,** 1576–1578 (1996).
28. Piao, S. *et al.* Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* **451,** 49–52 (2008).
29. Liao, C. *et al.* Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* **177,** 706–714 (2008).
30. Chapin, F. S. Nitrogen and phosphorus nutrition and nutrient cycling by evergreen and deciduous understory shrubs in an Alaskan black spruce forest. *Can. J. For. Res.* **13,** 773–781 (1983).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions J.D.F. designed the study, supervised data collection, performed the analyses and wrote the paper.

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METHODS

Study design and focal species. In 2006–2007 I established an experimental shade garden in Syracuse, New York, USA (43°03′ N, 76°09′ W), including three replicate blocks of 73 deciduous shrub and liana species (Supplementary Table 1). Species included congeners of eight genera (*Berberis*, *Celastrus*, *Elaeagnus*, *Euonymus*, *Frangula*, *Lonicera*, *Rhamnus*, *Viburnum*) for which there exists at least one species native to forests of the EUS and one non-native invader present in EUS forests or woodlands (see ref. 16 for details on habitat designations and 'non-native' and 'invader' criteria). A ninth species group consisted of common native EUS forest shrubs lacking EUS non-native invasive congeners. Transplants of most individuals were planted in 2006–2007, although a few were obtained in subsequent years; individuals were not monitored the year they were transplanted. Transplants were collected from the wild in central New York where possible (20 native and 9 non-native species); those absent from wildlands in the region were obtained from commercial growers of roughly the same latitude (including Forestfarm Nursery, Williams, Oregon, and Musser Forests, Indiana, Pennsylvania; seven species could be found only from southern US sources, including four natives and three non-natives; Supplementary Table 1). Individuals were spaced approximately 1 m apart beneath a wooden frame structure supporting 80% knitted black polypropylene shade cloth (DeWitt), deployed seasonally to coincide with local dates of forest canopy closure (approximately 20 May) and canopy leaf fall (approximately 24 October). This light regime approximates deciduous woodland conditions (midday PPFD measurements on a clear day under the shade cloth near the summer solstice peaked around 350 μmol $m^{-2}\,s^{-1}$, well above understory light levels in a mature, stratified temperate deciduous forest[31]) and was chosen as a compromise between light levels too high for forest conditions and too low to promote significant short-term growth. Estimates of percentage carbon gain before and after shade cloth placement are therefore conservative for a heavy canopy, where summer photosynthetic gain is expected to be lower than that observed in this study. For those species whose growth phenology has been examined elsewhere at a similar latitude, the behaviours displayed in the Syracuse garden were similar (including *Lonicera* × *bella* and *Rhamnus cathartica*[5], *Viburnum lantanoides*[13], *Lindera benzoin*[6] and *Berberis thunbergii*[9]), suggesting the patterns reported here are widely applicable to north-temperate latitudes. Neutral shade under polypropylene is also enriched in red:far-red ratio compared with natural forest understories; however, shade-tolerant plants like those used in the present study have been shown to be relatively insensitive to red:far-red ratio[32]. In several cases species-level replication was reduced by mortality, including ten species in the present study that were represented in only one block (Supplementary Table 1). Because comparisons of the attributes of particular species are not the focus of the present study, these data were retained for overall comparisons of native and non-native groups and statistical results were checked for dependence on the inclusion of one-replicate species. An additional target species, the EUS native *Berberis canadensis*, was excluded from the present study because garden individuals are suspected to be hybrids of *B. canadensis* and *B. thunbergii*.

Leaf budbreak. From 2008 onwards, we monitored spring bud and leaf development on each plant by photographing select nodes at 2- to 5-day intervals from early March to mid May. Buds from each image were classified according to five development stages: (1) dormant; (2) active (apparent bud swelling, scale development, visibility of inner scales, or scales changing in colour); (3) exposed (inner bud tissue apparent, including secondary cataphylls, transitional leaves, or tips of first leaves; first leaf reflexion in species lacking bud scales); (4) broken (general loosening of all bud structures including inner leaves, some exposure of leaf lamina; second leaf reflexion in species lacking bud scales); and (5) flushed/true leaf (full laminar surface of true leaf visible). Distributions of the timing of bud development across years and for native and non-native species were non-normal and compared by Mann–Whitney *U*-tests[33] with *P* values adjusted for multiple testing across years[34].

Leaf demography and senescence. We selected five healthy terminal branches at random on each individual (maximum 15 branches per species per year) before budbreak in early spring to monitor leaf production and senescence at 2 week intervals, with initial leaf emergence monitored at 3-day intervals to capture rapid spring development. Total extant leaves on existing buds and new shoots on each branch were counted at each interval. A new leaf was counted once it had reflexed by 20°, and leaf 'death' was defined as greater than 50% chlorosis. Branches damaged by herbivory or inadvertent breakage were excluded from further analysis. Leaf Chl content for select leaves was measured with a Chl meter (CCM-200, Opti-Sciences) by averaging three to five readings per leaf (avoiding the midrib) from July to December in 2009 and throughout the growing season in 2010. The CCM-200 measures the ratio of radiation transmitted through the leaf at wavelengths of 940 and 660 nm. Tests[35] indicate a correlation of CCM-200 index readings and total leaf Chl of $R^2 > 0.95$. Where possible, leaves were selected that emerged both before and after shade cloth placement. Leaf Chl data were pooled across 2009 and 2010 for analysis. For each monitored leaf, Chl values for standardized dates (15th of each month, May–November) were linearly interpolated from time series data, and species means were relativized separately for sun and shade leaves by their maximum Chl index reading (values between 0 and 1). Means and standard errors were then calculated separately for sun and shade leaves across native and non-native groups. Overall correlates of Chl content were tested in a mixed effects model using all 615 leaves monitored, using 'nativity' and 'sun/shade' as main effects and 'species' and 'year' as random effects[36].

Seasonal photosynthesis. Net leaf photosynthetic rates were monitored on a monthly basis (2008–2010) on a leaf of each individual using photosynthetic light curves (LI-COR 6400 with red–blue light-emitting diode light source, LI-COR Biosciences). We used a customized program (400 μmol CO_2 mol^{-1}, 700 μmol s^{-1} flow rate, 20 °C) that logged at 20-s intervals, starting with equilibration for four minutes at 800 μmol photon $m^{-2}\,s^{-1}$ and descending to 300, 100 and 50 for 2 min each, which preliminary trials in 2007 suggested was sufficient for leaf equilibration to different light levels. Measurements were taken daily on a species-rotating basis between 9:00 and 12:00 with replicate individuals of each species done on the same day. Mean photosynthetic rate of each species at high (800) and low light (100 PPFD) was modelled for season (before 20 May, 20 May to 24 October, after 24 October, averaged across years) and nativity in a linear mixed-effects model including season and species as random effects[36]. *A priori* multiple comparisons of native-non-native contrasts for each season were tested for significance using the simultaneous testing procedure of ref. 37.

Photosynthesis data were interpolated to hourly estimates over the growing season using the following procedure. For each measurement interval, light curve data were fitted to the four-parameter non-rectangular hyperbolic function[38] describing net CO_2 uptake (A) in units of μmol CO_2 $m^{-2}\,s^{-1}$:

$$A = \left\{ \mathrm{AQY} \times \mathrm{PPFD} + A_\mathrm{m} - \sqrt{(\mathrm{AQY} \times \mathrm{PPFD} + A_m)^2 - 4 \times \alpha \times \mathrm{AQY} \times \mathrm{PPFD} \times A_m} \right\} \Big/ 2\alpha - R_\mathrm{d}$$

where AQY is apparent quantum yield, PPFD is irradiance (μmol $m^{-2}\,s^{-1}$), A_m is maximum photosynthetic rate, R_d is dark respiration, and α is a unitless shape parameter describing curve convexity. To take advantage of all 30 values from the above light curve program (10 min of 20-s intervals) to maximize the robustness of model fit, I used nonlinear quantile regression[39] to estimate parameter values by fitting the 95th quantile rather than the mean response, reflecting the tendency of photosynthesis rates to equilibrate gradually to a maximum for each PPFD level. This procedure produced very high goodness-of-fit values as assessed by model residuals and fitted values (median R^2 of 2,100 curves = 0.98). In this way mean and standard errors for AQY, A_m, R_d and α were estimated for all species for each month leaves were present during the years of measurement (note that not all species were monitored in all years; mean $n = 24$ for each parameter per species). These parameter values were then used to model seasonal variation in AQY, A_m and R_d by interpolation using a regression spline generalized additive model[40] relating Julian date to each parameter, with values weighted by their precision (standard error^{-1}). Daily estimates of AQY, A_m and R_d (mean and standard error) were used in the carbon assimilation estimates (for species means see Supplementary Table 1). The shape parameter α varied little seasonally and was represented by its overall species mean.

Daily carbon gain estimates. The contribution of net photosynthetic activity in early spring and late autumn to total annual carbon gain was estimated for each species by stochastically simulating potential carbon assimilation over each day of the growing season. Given leaf-level photosynthetic properties and total leaf area of a particular species on Julian day t, and a diurnal light regime for day t at plant level from light sensor data, the simulation estimated whole-plant potential carbon gain over a 24-h period. The simulation was stochastic because all parameters (except for PPFD) were treated as random variables, with photosynthetic parameters sampled from their estimated daily distributions (see above) and daily leaf area estimates derived from empirical distributions of branch leaf counts. Daily peak PPFD values (2008–2010) from an LI-COR quantum sensor outside the period of shade cloth placement (full sun) were fitted to a daily model describing the linear increase or decrease of PPFD between winter and summer solstices[41], assuming clear-sky conditions. A similar model was fitted to light sensor data under the shade cloth (20 May to 24 October), with a rise in PPFD to the 21 June maximum and a decline (of equal rate) thereafter. The full seasonal PPFD curve is shown in Supplementary Fig. 3. Peak daily PPFD values were then used to interpolate light values to 30 min intervals throughout

the year using local sunrise, sunset and solar noon data, by means of linear regression (0 PPFD at sunrise to peak PPFD at solar noon, then back to 0 at sunset). For each day a plant had functional leaves, it assimilated carbon according to the function:

$$\text{daily C gain (in grams)} = \sum_{i}^{1-48} \text{area} \times L \times f(\text{PPFD}_i, A_\text{m}, R_\text{d}, \text{AQY}, \alpha) \times 1800 \times (12 \times 10^{-6})$$

where area is the area of a fully expanded leaf, L is the number of extant functional leaves on day t and f is the above non-rectangular hyperbolic function, including PPFD levels for each 30-min interval (i). The constants convert seconds to 30 min intervals and μmol to grams. Photosynthesis parameters AQY, A_m, and R_d were sampled randomly from a normal distribution of mean and standard error fitted from the above daily generalized linear model interpolation, and area and α were sampled from normal distributions using their overall means and standard errors (leaf areas included 5–10 samples per species). Owing to the large variability in leaf production per branch for most species, L was sampled from the empirical distribution of daily leaf counts across branch–years. The simulation included 1,000 permutations of annual trajectories of daily carbon gain for each species. Two native species, *Lonicera hirsuta* and *Shepherdia canadensis*, were strong positive outliers in the distribution of relative spring C gain (both near 50%), owing to all replicates showing very early leaf fall in 2010 (mid July), possibly the result of insect herbivory (*S. canadensis*) and powdery mildew (*L. hirsuta*). So as not to bias the native distribution of C gain phenology as a result of pest damage, these species were removed from C gain analysis. This had no qualitative effect on native–non-native C gain comparisons.

31. Canham, C. D. *et al.* Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20,** 620–631 (1990).
32. Morgan, D. C. & Smith, H. A. systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* **145,** 253–258 (1979).
33. Hothorn, T. & Hornik, K. exactRankTests: exact distributions for rank and permutation tests. R package version 0.8-19 (2010).
34. Hochberg, Y. A sharper Bonferroni procedure for multiple tests of significance. *Biometrika* **75,** 800–802 (1988).
35. Richardson, A. D., Duigan, S. P. & Berlyn, G. P. An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytol.* **153,** 185–194 (2002).
36. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Development Core Team. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-102 (2011).
37. Hothorn, T., Bretz, F. & Westfall, P. Simultaneous inference in general parametric models. *Biometrical J.* **50,** 346–363 (2008).
38. Lambers, H., Chapin, F. S. & Pons, T. L. *Plant Physiological Ecology* (Springer, 1998).
39. Koenker, R. quantreg: Quantile Regression. R package version 4.44 (2009).
40. Wood, S. N. Fast stable direct fitting and smoothness selection for generalized additive models. *J. R. Stat. Soc. B* **70,** 495–518 (2008).
41. Hutchison, B. A. & Matt, D. R. The distribution of solar radiation within a deciduous forest. *Ecol. Monogr.* **47,** 185–207 (1977).