






## LETTER

# Fast but steady: An integrated leaf-stem-root trait syndrome for woody forest invaders

Jason D. Fridley<sup>1</sup>  | Taryn L. Bauerle<sup>2</sup> | Alaã Craddock<sup>1</sup> | Alex R. Ebert<sup>1</sup>  |  
Douglas A. Frank<sup>1</sup>  | J. Mason Heberling<sup>1</sup>  | Elise D. Hinman<sup>1</sup> | Insu Jo<sup>1</sup>  |  
Kelsey A. Martinez<sup>1</sup> | Maria S. Smith<sup>2</sup> | Lauren J. Woolhiser<sup>1</sup> | Jingjing Yin<sup>2</sup>

<sup>1</sup>Department of Biology, Syracuse University, Syracuse, New York, USA

<sup>2</sup>School of Integrative Plant Sciences, Cornell University, Ithaca, New York, USA

**Correspondence**

Jason D. Fridley, Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13244, USA.  
Email: fridley@syr.edu

**Present address**

Alaã Craddock, Department of Biology, Onondaga Community College, 4585 West Seneca Turnpike, Syracuse, New York 13215, USA

J. Mason Heberling, Section of Botany, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213, USA

Elise D. Hinman, Utah Department of Environmental Quality, 195 N 1950 W, Salt Lake City, Utah 84116, USA

Insu Jo, Manaaki Whenua – Landcare Research, 54 Gerald Street, Lincoln, 7608, New Zealand

Maria S. Smith, Department of Horticulture and Crop Science, The Ohio State University, Ohio Agricultural Research and Development Center, 1680 Madison Ave, Wooster, Ohio 44691, USA

Jingjing Yin, Cornell Cooperative Extension of Chemung County, 425 Pennsylvania Avenue, Elmira, New York, USA

**Funding information**

Syracuse University; National Science Foundation, Grant/Award Number: IOS-1754273

Editor: Marcel Rejmanek

**Abstract**

Successful control and prevention of biological invasions depend on identifying traits of non-native species that promote fitness advantages in competition with native species. Here, we show that, among 76 native and non-native woody plants of deciduous forests of North America, invaders express a unique functional syndrome that combines high metabolic rate with robust leaves of longer lifespan and a greater duration of annual carbon gain, behaviours enabled by seasonally plastic xylem structure and rapid production of thin roots. This trait combination was absent in all native species examined and suggests the success of forest invaders is driven by a novel resource-use strategy. Furthermore, two traits alone—annual leaf duration and nuclear DNA content—separated native and invasive species with 93% accuracy, supporting the use of functional traits in invader risk assessments. A trait syndrome reflecting both fast growth capacity and understory persistence may be a key driver of forest invasions.

**KEYWORDS**

forest dynamics, growth-survival trade-off, invasion risk assessment, invasion success, leaf phenology

**INTRODUCTION**

Plant resource-use strategies involve the acquisition and allocation of energy and nutrients above- and belowground, and are a principal driver of community

assembly and ecosystem dynamics (Grime, 2006; Lavorel & Garnier, 2002; Reich, 2014). Whether such strategies differ between invasive species and their native competitors is a key question in the study of biological invasions, because differences in resource use

may determine the invasibility of communities and the impacts of invaders on ecosystem processes (Vilà et al., 2011). For example, there is strong evidence that invaders of disturbed, resource-rich habitats express functional traits associated with rapid resource acquisition and fast life history (Baker & Stebbins, 1965; Pyšek & Richardson, 2007; Rejmánek & Richardson, 1996). Compared to co-occurring native species, invaders often have higher specific leaf area (SLA), photosynthetic capacity at saturating light (Asat) and leaf nitrogen (N) content (Grotkopp & Rejmánek, 2007; Guo, 2018; van Kleunen et al., 2010). These traits contribute to high growth capacity, an attribute commonly associated with a competitive advantage in disturbed habitats of high light and nutrient availability (Adler et al., 2014; Grime, 2006). However, the bias towards acquisitive functional traits in invaders is, by itself, an unlikely explanation of species invasiveness in most habitats (Moles et al., 2012). In particular, there is increasing recognition that relatively undisturbed, low-resource ecosystems are also susceptible to invasions (Funk, 2013; Funk & Vitousek, 2007; Martin et al., 2009), and natural selection in these habitats typically favours traits that contribute to survival rather than high growth rate per se (Adler et al., 2014; Poorter et al., 2008). Although there is some evidence that such invaders express traits that facilitate both growth and survival advantages over native species (Closset-Kopp et al., 2007; Martin et al., 2010), the basis of invader competitive advantage in low-resource ecosystems remains poorly understood (Funk, 2013). As such ecosystems often act as refuges for native biodiversity (Huston, 1993), resolving mechanisms of invader advantage in these systems is particularly important for conservation (Funk et al., 2020).

A case in point is the growing threat of plant invaders in closed-canopy forests worldwide (Martin et al., 2009). Although canopy disturbance is a well-established driver of forest population dynamics (Canham, 1985; Pacala et al., 1996), many woody invaders of both temperate and tropical forests can establish in shade and/or persist as saplings for extended periods after canopy closure (Closset-Kopp et al., 2007; Greenberg et al., 2001; Hoyos et al., 2010; Loh & Daehler, 2007; Yamashita et al., 2003). Unexpectedly, some of these low-light invaders also express acquisitive leaf traits (Heberling & Fridley, 2016) and grow faster than co-occurring native species in high light, such as in canopy gaps (Bellingham et al., 2018; Herron et al., 2007; Martin et al., 2010; Yamashita et al., 2003). How invaders achieve this combination of fast growth and shade tolerance remains unknown. Although leaf traits associated with growth rate are relatively easy to measure and widely available for native-invader contrasts (van Kleunen et al., 2010), traits that contribute to stress tolerance and survival, such as leaf lifespan (Hallick et al., 2009; Poorter & Bongers, 2006), are rarely measured (Funk, 2013). Moreover, although theory (Givnish, 2002; Grime, 2006) predicts that leaf

traits reflect nutrient supply rates and root foraging behaviour, empirical integration of above- and below-ground functioning in invasion studies remains rare (Jo et al., 2015), making it difficult to interpret the significance of leaf traits alone to invader success.

Shade tolerance can be conferred on woody plants in temperate deciduous forests by early leaf out and/or late leaf senescence, leading to spring and fall subsidies of high rates of carbon gain that can permit tolerance of sites that are densely shaded in midsummer (Augsburger, 2008; Givnish, 2002; Lopez et al., 2008). Early leaf out and late senescence are both promoted by narrow xylem conduits that are resistant to frost-induced cavitation (Givnish, 2002). Deciduous forests may thus be especially prone to invasion if introduced species take advantage of early- and late-season canopy openness (Donnelly & Yu, 2021; Fridley, 2012; Gallinat et al., 2015). However, the physiological mechanisms enabling such extended leaf duration remain unclear. Lechowicz (1984) introduced the idea of phylogenetic constraints on xylem anatomy and freezing tolerance as a potential driver of spring foliar phenology, indicating evolutionary history may influence the phenological strategies of co-occurring species. A similar mechanism was suggested by Zohner and Renner (2017) that invokes the role of historical climatic variability in the timing of spring budbreak, which varies across continents and may drive phenological differences between co-occurring native and invasive species (Zohner et al., 2017). On the other hand, phenological differences between native and invasive species are often stronger in autumn than in spring (Fridley, 2012; Gallinat et al., 2015), and there are few explanations for delayed invader leaf senescence (Heberling et al., 2016; Yin et al., 2015). One possibility is that leaf phenological strategies are one component of whole-plant carbon and nutrient dynamics that are driven in part by belowground processes, including nutrient uptake capacity (Jo et al., 2015) and energy storage in the form of non-structural carbohydrates (Hinman & Fridley, 2018), but few if any studies have addressed resource-use strategies of native and invaders at the whole-plant scale.

We compared the functional strategies of native and invasive woody species present in the understorey of deciduous forests of North America, where non-native invasive shrubs and lianas pose significant threats to natural and managed ecosystems (Webster et al., 2006). Our study included 44 native species and 32 non-native, naturalised species, 24 of which are managed as invaders of rapid spread and high ecological impact (Dataset S1). The remaining eight non-native focal species are naturalised in North America but not presently managed as invaders ('naturalised-only'). We use 'nativity' to refer to contrasts of native versus all non-native species, and 'invasive status' to refer to contrasts of native species versus only those non-native species classified as invaders. Species were selected to facilitate phylogenetically

independent contrasts, with native-invader comparisons present across eight angiosperm genera. Trait measurements were conducted in a common garden in Syracuse, New York (USA), with individuals planted in three replicate shade structures simulating a seasonally light-limited forest understorey. Traits (Dataset S2) included aspects of leaf metabolism, chemistry and morphology; root and stem functional traits; whole-plant attributes including root and shoot production, growth phenology, and non-structural carbohydrate dynamics; and nuclear DNA content, an integrative trait that is associated with both plant growth rate and spring foliar phenology (Fridley & Craddock, 2015). We addressed the following questions: (1) What are the dominant relationships of traits related to resource-use strategies in deciduous woody species? (2) What is the relationship of leaf functional traits to root and stem traits? (3) Do native and non-native, invasive species differ in whole-plant functional trait strategies—i.e. is there evidence for an invader trait syndrome? (4) Which traits most strongly discriminate between native and invasive species?

## MATERIALS AND METHODS

### Focal species

Our 76 focal species (Dataset S1) were chosen to contrast the ecological behaviours of common woody, non-native invasive species of deciduous forests of North America (NA) with that of co-occurring native species. At the time of species selection (2006), few physiological studies had been conducted on NA native and invasive shrubs (Harrington et al., 1989), and we had little to no information on leaf properties, branching strategies, xylem anatomy or root behaviour of our focal species. Our selection of woody understorey invaders includes nearly all those managed as high-impact invaders in the Northeast U.S. (Fridley, 2008). To select appropriate native species, we considered both their ecological importance and their phylogenetic relatedness to invaders, to protect against misinterpretation of trait differences as a result of evolutionary distance alone. Although some species are classified primarily as small trees, we excluded species that attain canopy status because forest invasions in NA are strongly biased towards understorey shrubs and lianas (Fridley, 2008; Webster et al., 2006). Growth form classifications of all focal species therefore included 'shrub' or 'vine' (USDA & NRCS, 2020). The only habitat consideration was that a species be documented as present in forests somewhere across its NA range; some species are more common in open habitat or forest edges but all are tolerant of at least partial shade. We included species endemic to more southern regions in NA if hardy to horticultural zone 5 of Syracuse, NY.

We treated species as non-native if they were introduced to NA after 1500 C.E. Of the 32 non-native species,

24 are managed as invaders by one or more U.S. management agencies because they (1) have spread naturally and widely from points of introduction (Fridley, 2013), and (2) have impacted native populations (Fridley, 2008). We treat eight non-native focal species as naturalised rather than invasive, because they remain uncommon more than a century after introduction and have not been placed on management agency invasive lists. However, all eight naturally regenerate in NA (USDA & NRCS, 2020). These naturalised species are from taxonomic groups that also contain focal native and invasive species. The separation of non-native species as invasive versus naturalised-only facilitates the identification of traits associated with competitive ability and ecological impact, rather than only recruitment and persistence in the understorey.

### Common garden

We established a common garden in 2006 on the campus of Syracuse University, Syracuse, New York, USA (43°39'N, 76°99'W). The garden had been maintained previously as lawn on pH-neutral, well-drained loamy soil. We planted three individuals of most species in 2006 and 2007 in three replicate blocks, each artificially shaded by neutral black shade cloth (20% light transmittance) from late May to late October. Seasonal light levels are reported in Martinez and Fridley (2018). Individuals were typically 1–2 years old at the time of planting and <50 cm tall, planted 2 m apart and sourced from the wild in central New York where possible or from commercial growers of similar latitude (Dataset S1).

### Trait data

Traits are summarised in Dataset S2. Many traits used in the present analysis are described in prior studies (listed in Dataset S2); for a summary of these measurements and details of new trait measurements refer to Appendix S1. Because a given trait may have been measured in multiple years, we estimated species-level trait means using a random effects model that included 'species' and 'year' effects (Appendix S1). We removed highly correlated variables prior to analysis and created a single spring 'leafout' date variable (Appendix S1). Our final species-trait matrix included 68 continuous traits for 76 species (Dataset S2). Most leaf morphology, phenology and photosynthetic data based on light curves were available for >95% of the species pool. Xylem anatomy, leaf and root chemistry, and DNA content were available for 75% or more species. Root traits, in general, were less well represented across species, although specific root length (SRL) (71%), tissue density and decomposition rate were available for >60%. The traits of lowest coverage were root production (32%), annual leaf area produced (32%)

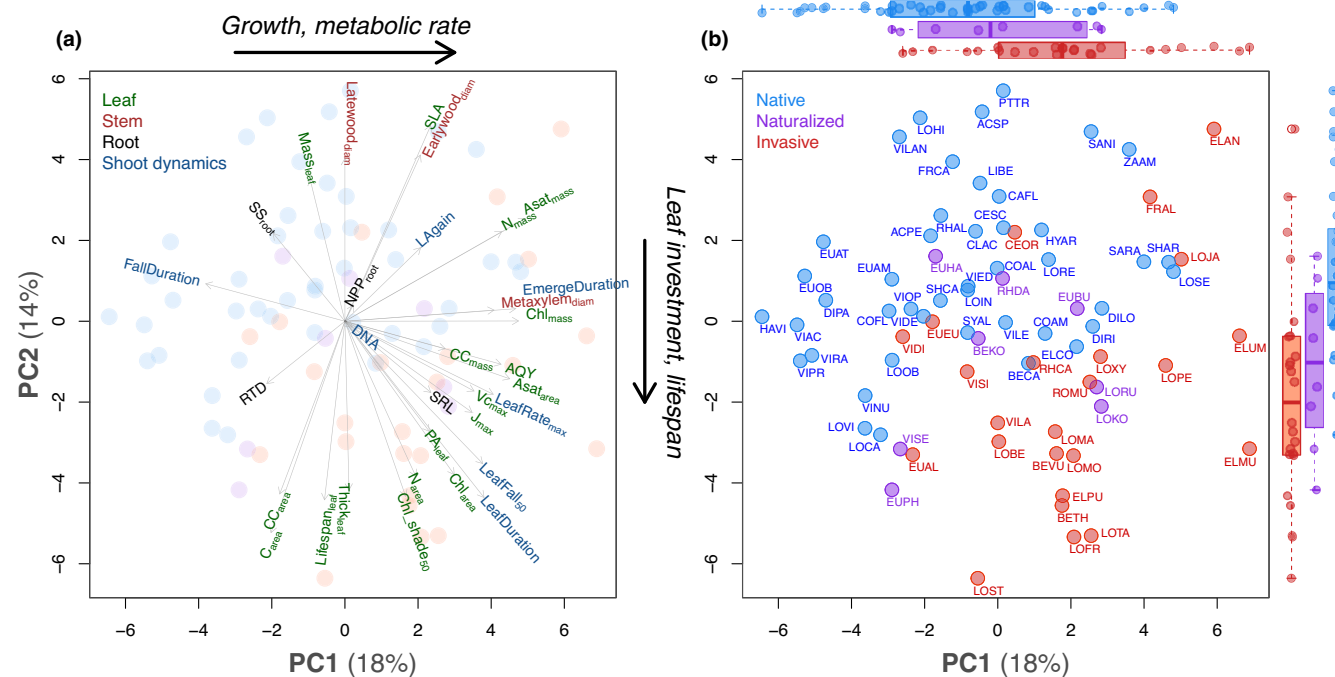
and several photosynthetic parameters ( $V_{c,max}$ ,  $J_{max}$ , light saturation point; 40%). Thirty-seven traits showed substantial right skew and were log-transformed for analysis.

## Statistical analyses

All statistical analyses were performed in R 3.6.3 for Windows (R Core Team, 2020). We applied phylogenetically independent contrasts using a correlation matrix of phylogenetic distances calculated with an aged tree based on the species-level phylogeny of Jo et al. (2016). Of our 76 focal species, 10 species were added to the Jo et al. (2016) phylogeny, including four (*Acer spicatum*, *Clethra acuminata*, *Lonicera hirsuta*, *L. korolkowii*) from the phylogeny of Fridley and Craddock (2015). The remaining six species were placed in the phylogeny using the most up-to-date familial/generic phylogenies, including those for *Berberis canadensis* (Kim et al., 2004), *Elaeagnus* and *Shepherdia* (Bartish et al., 2002; note several *Elaeagnus* species remain unresolved), *Symphoricarpos album* (Bell & Gonzalez, 2019) and *Viburnum lantanoides* and *V. nudum* (Clement & Donoghue, 2012).

We performed a principal components analysis on a trait matrix of 76 species and 68 continuous variables with variables scaled to zero mean and unit variance. Missing values (29% of the trait matrix) were imputed

using probabilistic PCA (PPCA). PPCA estimates missing values from a multivariate normal distribution fit to observed values, and is one of several commonly used multivariate imputation methods for trait data, including Bayesian PCA (BPCA), iterative PCA (IPCA) and joint modelling (JointM) (Dray & Josse, 2015; Stacklies et al., 2007). Of these, PPCA has also been shown to perform without bias in sparse datasets of more than 30% missing values (Stacklies et al., 2007), did not require strong priors, and was stable across the optimal number of principal components for imputation. Furthermore, because imputed values of PPCA are fit closer to the centre of the empirical distribution of each trait than the other methods, use of PPCA is a conservative approach that down-weights the importance of traits that have a high frequency of missing values. We performed PPCA in R using the package ‘pcaMethods’ (Stacklies et al., 2007), using the suggested optimum of two principal components for imputation. We compared the distribution of each trait before and after imputation to confirm missing values were fit conservatively near the centre of observed values (Figure S1). To further confirm the robustness of the PPCA, we compared it to a more conservative PCA using a subset of 40 traits that were available for at least 2/3 of the 68 target species, with results equivalent to that reported in Figure 1 (Figure S2). The distribution of native and non-native species, or native/naturalised/



**FIGURE 1** Principal component analysis of 68 continuous traits across 76 species, illustrating the association of forest plant invaders with both fast metabolism and growth rate (high values of PC axis 1) and high leaf longevity (low values of PC axis 2). (a) Vectors of 32 traits along the first two principal components, with traits coloured by tissue type. Traits are described in Dataset S2; those not defined in the text included leaf perimeter-to-area ratio ( $PA_{leaf}$ ), root tissue density (RTD), maximum rates of electron transport ( $J_{max}$ ) and carboxylation ( $V_{c,max}$ ) and annual leaf area gain ( $LA_{gain}$ ). Traits not shown are those that did not rank in the top 10 loadings on either axis or were not among the top 20 distinguishing native and invasive species; relationships of all 68 traits are shown in Figure S4. (b) Species' scores along with axis quartile and range distributions of native (blue,  $N = 44$ ), naturalised (purple,  $N = 8$ ) and invasive (red,  $N = 24$ ) species. Species names are listed in Figure 3

invasive groups, along PCs 1 and 2 were contrasted with ANOVAs, and the overall separation of groups in trait space was tested with PERMANOVA of a Gower-based distance matrix using the `adonis` function of the R package ‘vegan’ (Oksanen et al., 2019), after ensuring multivariate homogeneity of group dispersions using the `vegan` `betadisper` function. Use of Gower distance allowed a conservative approach to testing multivariate group differences because it is robust to missing values and thus did not require the use of imputed trait values.

We estimated the mean effect size of nativity on each trait in phylogenetic generalised least squares (PGLS) regression. We conducted PGLS with the `gls` function in the R ‘nlme’ package (Pinheiro et al., 2020), using a correlation matrix derived from species’ phylogenetic distances from the aged phylogeny, assuming a Brownian motion model of evolutionary change. We also estimated phylogenetic signal (Pagel’s  $\lambda$ ) for each trait, from 0 (phylogenetic independence) to 1 (traits evolve according to Brownian motion), using the ‘`phylosig`’ function of the R ‘`phytools`’ library (Revell, 2012; note the estimation of Pagel’s  $\lambda$  is zero for those few traits of  $N < 30$ , suggesting a potential artefact of analysis). We compared PGLS effect sizes to those of ordinary least squares regressions that ignore phylogenetic autocorrelation (Figure S3). We performed tests with and without the eight naturalised-only species. We report mean effect sizes along with 95% confidence intervals for linear models using coefficient standard errors. Significance tests of pairwise comparisons of trait values across native and non-native (or native and invasive) species were corrected for multiple testing following Benjamini and Hochberg (1995).

To find a small number of potentially interactive traits that best discriminated between native and invasive species, we used boosted regression tree (BRT) analysis in the R packages ‘`dismo`’ (Hijmans et al., 2017) and ‘`gbm`’ (Greenwell et al., 2019). We followed Elith et al. (2008) with a bag fraction of 70%, a slow learning rate (0.005) and a convergence number of trees over 1000, and we chose a low complexity parameter that conservatively allowed for only 2-way interactions. We simplified a fitted model that included all 68 traits by means of cross-validation, using the `gbm.simplify` function of ‘`dismo`’, as described by Elith et al. (2008).

## RESULTS

### Whole-plant trait relationships

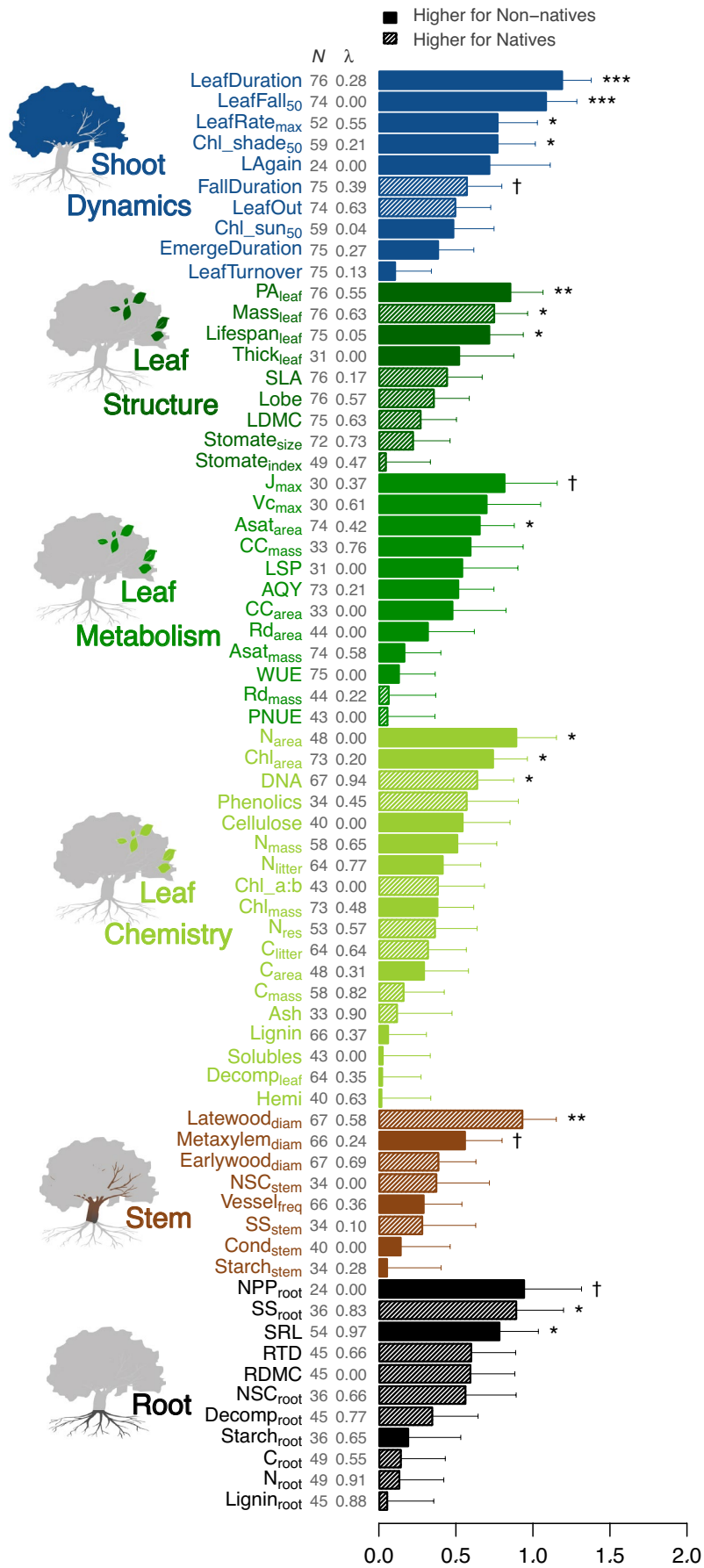
We found two primary axes of trait variation that explained 1/3 of the overall variance of 68 traits across 76 species (principal components analysis, Figure 1a and

Figure S4; eigenvalues for PC1 and 2, 18% and 14% respectively; trait loadings in Dataset S2). PC1 reflected traits associated with the instantaneous rate of carbon (C) gain, including high photosynthetic rate ( $Asat_{mass}$ ,  $Asat_{area}$ ) and leaf nutrient content ( $N_{mass}$ ,  $Chl_{mass}$ ), along with the rate of leaf production ( $LeafRate_{max}$ ). PC2 separated species of large ( $Mass_{leaf}$ ), thin (high SLA) and short-lived leaves from those of thick ( $Thick_{leaf}$ ), long-lived ( $Lifespan_{leaf}$ ) leaves of high energy and nutrient investment per unit area (construction cost,  $CC_{area}$ ; C and N content,  $C_{area}$ ,  $N_{area}$ ). Primary trait axes were also associated with growth phenology and xylem anatomy. The size of metaxylem vessels ( $Metaxylem_{diam}$ ), which support the first cohort of leaves in spring, was positively associated with PC1, while the size of xylem vessels created in summer and autumn ( $Earlywood_{diam}$ ,  $Latewood_{diam}$ ) was associated with large-leaved species of high PC2 values. In addition, species that scored high on PC1 showed indeterminate (i.e. continuous) leaf growth (high  $EmergeDuration$  values) and a short duration of leaf senescence ( $FallDuration$ ), while species scoring low on PC2 showed late autumnal senescence (median date of leaf loss,  $LeafFall_{50}$ ; date of 50% chlorophyll loss,  $Chl_{shade}_{50}$ ) and a long annual period of C gain ( $LeafDuration$ , the number of days of live leaves per year). Thus, across all species in our analysis, we found a high degree of coordination of aboveground traits conferring high growth rate, associated with PC1, that were independent of leaf lifespan and construction cost (PC2). Root traits were not among those that loaded strongly on PC axes 1 or 2, although this may be due to their overall smaller sample size (max  $N = 54$ , for specific root length [SRL]).

### Trait differences between native and invasive species

Native and invasive species occupied different regions of trait space (PERMANOVA  $F = 6.24$  on 1, 66 df;  $p < 0.0001$ ; Figure 1b). Non-native species overall, as well as only those managed as invaders, were strongly skewed along both primary trait axes (Figure 1b,  $p < 0.0001$  in separate ANOVAs for PC1 and PC2). Naturalised-only species were intermediate along PC1 and grouped statistically with invaders on PC2 (Tukey HSD tests,  $p < 0.05$  for naturalised-native contrasts). No invasive species occupied the region of trait space representing slow growth potential and short leaf lifespan that characterised the majority of native species. We found a significant but weak negative correlation of PC1 and PC2 scores for

**FIGURE 2** Traits associated with invasiveness in woody understorey species of North America. Bars indicate mean + 95% CI standardised effect size of nativity on each trait, with filled bars indicating higher values for non-native species. Traits (see Dataset S2) are grouped according to tissue type. Text columns indicate the number of species measured for each trait and the trait’s phylogenetic signal (Pagel’s  $\lambda$ ). Symbols indicate the  $p$  value associated with the null hypothesis of no difference in trait means across native and non-native species, adjusted for multiple testing ( $***p < 0.001$ ,  $**p < 0.01$ ,  $*p < 0.05$ ,  $†p < 0.01$ ). Effect sizes for trait contrasts between native species and invasive species (excluding 8 naturalised-only species) are shown in Figure S5



native species (OLS regression,  $p = 0.055$ ,  $t = -1.97$  on 42 df,  $R^2 = 8\%$ ), but no such relationship for non-native or invasive species ( $p = 0.20$ ,  $0.17$ , resp.). Examined on a trait-by-trait basis with post-hoc corrections for multiple testing, about a fourth of the 68 traits showed a significant discrimination by both nativity (Figure 2) and invasive status (Figure S5). These included phenology variables (LeafDuration, LeafFall<sub>50</sub>), many leaf attributes associated with both PC1 and PC2 (photosynthetic parameters, N content, leaf mass, lifespan), root traits (annual root production [NPP<sub>root</sub>], specific root length [SRL]) and late-season xylem vessel size (Latewood<sub>diam</sub>).

Although phylogenetic relationships were associated with functional trait differences across species, they did not change our characterisation of how non-native or invasive species differ from native species. Species' scores for both PC1 and PC2 showed a significant phylogenetic signal ( $\lambda = 0.61$ ,  $0.55$ , resp.,  $p < 0.001$ ; Figure 3), and we found a weak but significant correlation of overall trait and phylogenetic dissimilarity (trait Gower distance, Mantel  $r = 0.16$ ,  $p < 0.001$ ). However, of those traits significantly associated with nativity, in only three cases (leaf size [Mass<sub>leaf</sub>], nuclear DNA content, Latewood<sub>diam</sub>) were effects sensitive to phylogenetic autocorrelation (Figure S3), and neither nativity ( $p = 0.07$ ) nor invasive status ( $p = 1.00$ ) showed significant phylogenetic signal.

### Indicator traits of invader syndrome

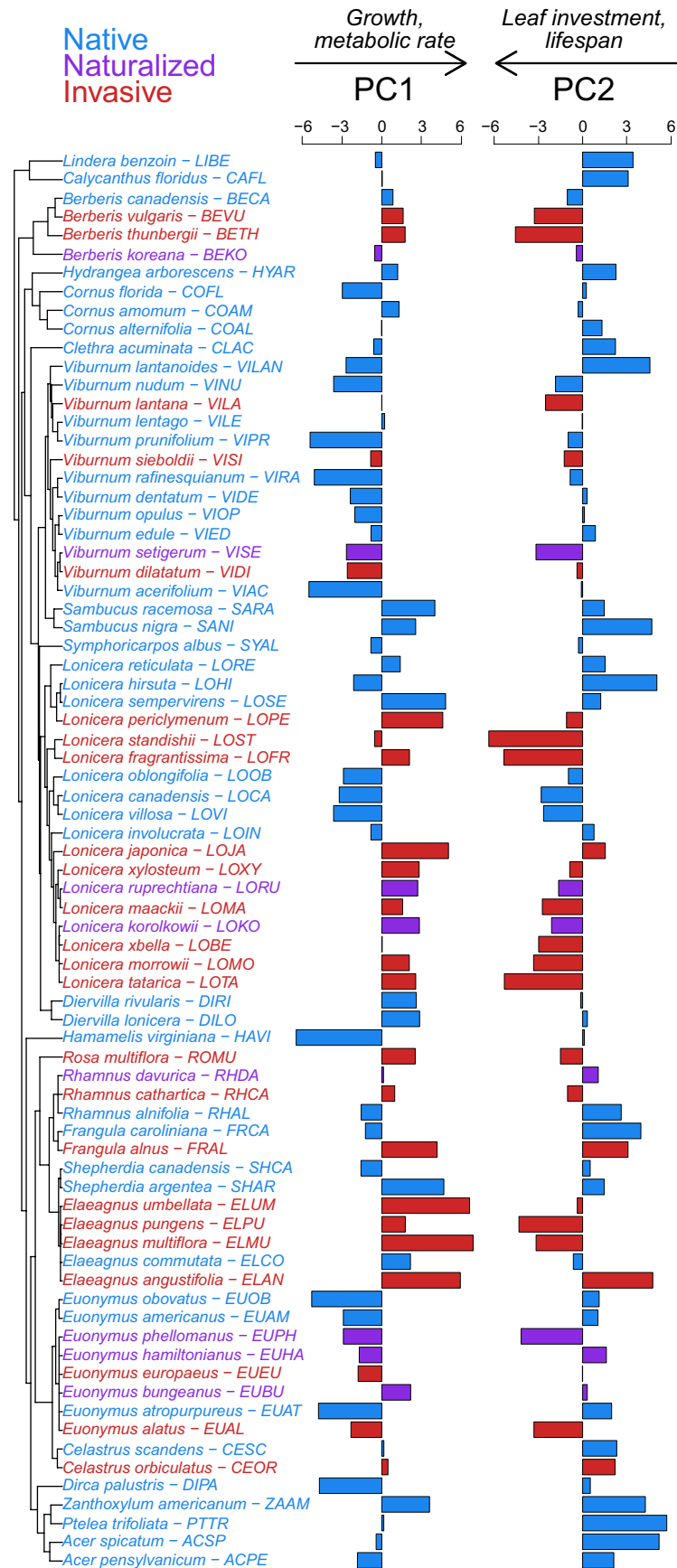
To identify a small set of traits that best discriminated between native and invasive (or all non-native) species, we used all 68 traits in a boosted regression tree (BRT) analysis. Best-fit BRT models separated native and non-native species with 95% accuracy ( $N = 76$ ; cross-validation AUC score = 0.912), and natives and invaders with 93% accuracy ( $N = 68$ ; cv AUC = 0.964), using only two traits: annual leaf duration and DNA content. The effect of both traits was nonlinear: nearly all invaders had live leaves present over 190 days per year, and typically contained less than 2 pg DNA (2C value) (Figure 4).

## DISCUSSION

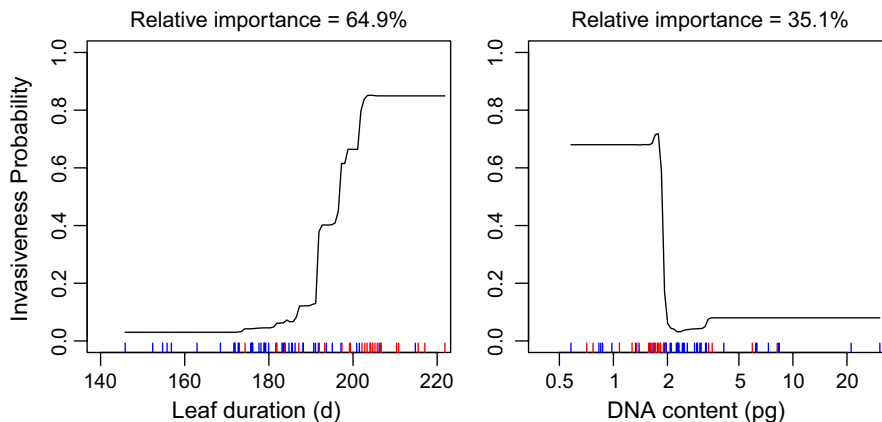
Our results point to a consistent 'invader syndrome' for introduced woody species in North American deciduous forests, independent of phylogeny. This syndrome is associated with a rapidly growing but shade-tolerant phenotype of resource use and C gain that combines rapid instantaneous growth potential—high C gain and leaf production when resources are abundant, particularly in spring—with a long duration of C gain per resource invested (leaf C, N), particularly late in the season from small, long-lived, N-rich leaves. Invasive understorey

plants in our study combine fast growth potential and a long growing season in a combination that does not occur in any of the 44 native species we examined. Early leaf out and late leaf senescence should enhance shade tolerance in woody plants in temperate forests and permit high rates of photosynthesis based on adaptation to high light levels before and after canopy closure (Givnish, 2002; Lopez et al., 2008). Furthermore, leaf traits of invaders appear to be integrated with stem and root traits that enable both an extended growing season and rapid spring growth. For example, metaxylem vessels in invaders are large enough to support high stomatal conductance in spring leaves, while latewood vessel diameter in these same species is relatively narrow to protect against freezing-induced embolisms in late autumn (Yin et al., 2015). Similarly, although late autumnal C gain in invaders induces significant leaf N losses due to lower leaf resorption (N<sub>litter</sub>), the strong association of higher SRL and fine root production (NPP<sub>root</sub>) in invaders may support higher rates of N uptake (Jo et al., 2015, 2017). In contrast, it remains unclear whether any of the functional traits we've measured to date would suggest a growth or survival advantage for native species in any ecological context. One potential fitness cost in invaders is their tendency to store less C in the form of non-structural carbohydrates (NSCs), particularly soluble sugars (SS<sub>root</sub>; Figure 2), but their functional role remains unknown (Hinman & Fridley, 2018). Furthermore, although some of our focal invaders are tolerant of very low light levels (Heberling & Fridley, 2016; Xu et al., 2007), it is likely that some of the native species at the conservative ends of our primary trait axes maintain a survival advantage over invaders in conditions of extreme shade (e.g. <3% sun; Martin et al., 2010).

Non-native invaders as a group exhibit leaf traits that, relative to native species, offer competitive advantages in both high-light (spring, open-canopy) and low-light (summer, closed-canopy) environments. Although we did not detect trait-based evidence for strong growth-survival trade-offs within native species, the absence of any native species expressing both fast growth and a long growing season as a result of high leaf investment begs explanation. One possibility is that the environmental history of North America has selected against deciduous lineages of long leaf duration as a result of unpredictable spring and autumn climate compared to much of Eurasia (Zohner & Renner, 2017), a hypothesis borne out in greater chilling requirements for budbreak in North American species (Zohner et al., 2017). Many Eurasian temperate forests also experience longer growing seasons as a result of maritime influences such as the Gulf Stream (Palter, 2015) that may predispose Eurasian lineages to extended leaf display. Second, an extension of the annual frost-free period for many regions of North America that has accompanied global climate change



**FIGURE 3** Phylogenetic distribution of primary trait axes 1 and 2 from principal components analysis, including native (blue), naturalised (purple) and invasive (red) species



**FIGURE 4** Leaf duration and DNA content distinguish native and invasive species. Boosted regression tree (BRT) partial dependence plots show the probability that a species is classified as invasive for a given value of leaf duration (days of live leaves per year) or DNA content (2C pg), averaging over effects of the other variable ( $N = 68$ ). Distributions of each variable are shown at the top (blue = native, red = invasive). BRT relative importance is the number of times the variable is selected for splitting, weighted by the improvement in model fit with each split and averaged over all trees

(Linderholm, 2006) has likely benefited invaders of long leaf duration more than native species (Mulder & Spellman, 2019; Wolkovich et al., 2013). However, as most of the invaders in our study have spread for over a century, recent climate change is unlikely to be the driver of the functional differences we document here. Third, if invaders lack specialist enemies from their native ranges, they may have reallocated some defensive resources towards growth while maintaining high investments in leaf structure. Although there is some evidence supporting release from predation by specialist insects in our target species (Lieurance & Cipollini, 2013; Schierenbeck et al., 1994), we are unaware of evidence suggesting recent selection towards longer leaf display or lifespan in North American invaders. Finally, by chance, we may have failed to include native species that express both fast growth and long leaf duration. Although we cannot exclude this possibility, we suspect the native-invader trait differences we report are general, as both higher productivity and extended foliar phenology of invaders relative to co-occurring natives has been reported across mesic North America (Morris et al., 2002; Mulder & Spellman, 2019; Xu et al., 2007).

Non-invasive, ‘naturalised-only’ non-native species were a relatively small component of our study species ( $N = 8$ ). Nonetheless, they expressed a consistent phenotype that supports the hypothesis that understorey invasiveness requires both shade tolerance and the capacity for rapid growth. Like invaders, naturalised-only species had longer-lived leaves and higher leaf investment than natives, as is typical for shade-tolerant understorey species (Hallik et al., 2009). However, unlike invaders, the traits of naturalised-only species associated with growth- and metabolic rates along PC1 were not significantly different from those of native species (Figure 1b). Although it is difficult to quantify historical introduction efforts of these species with current data, it is notable

that each has been present in North America for over a century (Dataset S1; Rehder, 1940). In contrast, many of the invasive species in our study escaped cultivation to become locally dominant in forests within a few decades of their introduction (Fridley, 2013). The lack of spread and slower growth capacity of naturalised-only species suggests that other more recently introduced species that share these traits may also have low invasive potential, but this pattern should be confirmed with similar trait measurements across a larger pool of non-invasive species of similarly long residence times.

Our study supports the use of functional traits in invasive species risk assessment. We identified two traits that, together, distinguished native and invasive species with over 90% accuracy. The result is notable because it is based only on resource-use traits, which typically play a minor role in invader risk assessments (Herron et al., 2007; Křivánek & Pyšek, 2006; Reichard & Hamilton, 1997). In our study, leaf duration is associated with greater annual carbon gain for invaders, which for woody species in North America has been more strongly linked to extended leaf function in autumn than spring (Fridley, 2012; Gallinat et al., 2015; but see O’Connell & Savage, 2020). As to the functional role of nuclear DNA content in predicting invasiveness, we suggest it is two-fold. Because our focal species included only two polyploids (*Lonicera sempervirens* and *L. periclymenum*), DNA content was driven by variation in genome size, which is a robust predictor of invasiveness across the plant kingdom, in part because selection for fast growth limits the accumulation of non-coding DNA (Suda et al., 2015). In seasonal habitats where the timing of spring emergence influences annual C gain, DNA content also has a positive association with fitness relating to cell size and the potential for rapid leaf expansion (Fridley & Craddock, 2015). Here, DNA content complements leaf duration in the prediction of invasiveness because it separates out

those native species that have long leaf duration from early budbreak (high DNA content) rather than late autumnal senescence due to long leaf lifespan (Fridley, 2012; Fridley & Craddock, 2015). Thus, for woody deciduous species, DNA content integrates trait strategies along both growth rate (low DNA) and leaf investment (low DNA and long leaf duration) trait axes. Because the DNA effect is nonlinear it is not associated with primary trait axes (Figure 1a); furthermore, its strong phylogenetic signal ( $\lambda = 0.94$ ) and lack of significance as a predictor of invasiveness in phylogenetic regression stems from high values for native species in our study that were taxonomically distant from invaders. Nonetheless, our analysis supports both DNA content and leaf duration as leading candidates for low-cost screening of the invasive potential of new introductions.

Our study is based on the ecology of temperate deciduous species, but several lines of evidence suggest the 'fast-but-steady' functional syndrome we document here is a common feature of forest invasions across temperate and tropical biomes. First, the combination of fast growth and long leaf lifespan is advantageous in both deciduous and evergreen forests due to the association of leaf lifespan with shade tolerance (Hallik et al., 2009; Poorter & Bongers, 2006). Second, although trait comparisons involving leaf lifespan are often lacking, many of the world's most aggressive forest invaders combine fast growth potential with high recruitment and persistence in the shade of an intact canopy (Martin et al., 2009); examples include woody invaders of mature tropical forests (*Miconia calvescens*, Meyer & Florence, 1996; *Psidium cattleianum*, Loh & Daehler, 2007; *Spathodea campanulata*, Larrue et al., 2014; *Pittosporum undulatum*, Bellingham et al., 2018), temperate and subtropical forests of South America (*Ligustrum lucidum*, Hoyos et al., 2010; *Hovenia dulcis*, Dechoum et al., 2015) and Asia (*Bischofia javanica*, Yamashita et al., 2003), and forests of central Europe (*Prunus serotina*, Closset-Kopp et al., 2007; *Quercus rubra*, Major et al., 2013). Third, despite the expectation of reduced investment in leaf structure or defence between home and away ranges (Müller-Schärer et al., 2004), some forest invaders in their away range build more robust leaves without apparent loss of photosynthetic or growth potential (Heberling et al., 2016; Shouman et al., 2017).

## CONCLUSION

Our results support a prevention strategy for forest invasions worldwide based on the screening of traits related to both growth capacity and leaf longevity. As the trait syndrome we document for North American invaders is consistent with growth and survival advantages of many global forest invaders in both temperate and tropical habitats, a general understanding of forest invasions

may rest on identifying physiological mechanisms by which invaders are able to avoid apparent growth-survival trade-offs commonly invoked for native woody species (Martin et al., 2010; Pacala et al., 1996). Because the spread of plant invaders in shaded habitats has generally lagged behind those of more disturbed ecosystems (Martin et al., 2009), the use of trait-based syndromes to reduce understory invasions presents a significant opportunity to protect global forest biodiversity (Novoa et al., 2020).

## ACKNOWLEDGEMENTS

We thank members of the Syracuse University Plant Ecology Lab, T. and R. Starmer for logistical support, and T. Givnish for valuable manuscript comments. This research was funded by Syracuse University, U.S. National Science Foundation graduate research awards to J.M.H. and E.D.H, and U.S. NSF grant IOS-1754273 to J.D.F.

## AUTHOR CONTRIBUTIONS

Jason D. Fridley conceptualised the study, conducted formal analysis, wrote the original draft and directed the project. All authors participated in data collection. Jason D. Fridley, Douglas A. Frank, J. Mason Heberling, Elise D. Hinman, Insu Jo and Kelsey A. Martinez edited the manuscript, and Jason D. Fridley and Insu Jo created the figures. Funding acquisition and supervision were provided by Jason D. Fridley, Douglas A. Frank and Taryn L. Bauerle.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13967>.

## DATA AVAILABILITY STATEMENT

Data and R code used for analyses are archived in Zenodo at <https://doi.org/10.5281/zenodo.5103459>.

## ORCID

Jason D. Fridley  <https://orcid.org/0000-0002-0581-376X>

Alex R. Ebert  <https://orcid.org/0000-0002-4023-1618>

Douglas A. Frank  <https://orcid.org/0000-0001-9271-0154>

J. Mason Heberling  <https://orcid.org/0000-0003-0756-5090>

Insu Jo  <https://orcid.org/0000-0002-1759-2319>

<https://orcid.org/0000-0002-1759-2319>

<https://orcid.org/0000-0002-1759-2319>

## REFERENCES

- Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. et al. (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 740–745.
- Augspurger, C.K. (2008) Early spring leaf-out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia*, 156, 281–286.

- Baker, H.G. & Stebbins, G.L. (Eds.) (1965) *The genetics of colonizing species*. New York, NY: Academic Press.
- Bartish, I.V., Jeppsson, N., Nybom, H. & Swenson, U. (2002) Phylogeny of Hippophaeae (Elaeagnaceae) inferred from parsimony analysis of chloroplast DNA and morphology. *Systematic Botany*, 27, 41–54.
- Bell, C.D. & Gonzalez, L.A. (2019) Historical biogeography and temporal diversification in *Symphoricarpos* (Caprifoliaceae, Caprifoliaceae, Dipsacales). *Systematic Botany*, 44, 83–89.
- Bellingham, P.J., Tanner, E.V., Martin, P.H., Healey, J.R. & Burge, O.R. (2018) Endemic trees in a tropical biodiversity hotspot imperilled by an invasive tree. *Biological Conservation*, 217, 47–53.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57, 289–300.
- Canham, C.D. (1985) Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club*, 112, 134–145.
- Clement, W.L. & Donoghue, M.J. (2012) Barcoding success as a function of phylogenetic relatedness in *Viburnum*, a clade of woody angiosperms. *BMC Evolutionary Biology*, 12, 73.
- Closset-Kopp, D., Chabrerie, O., Valentin, B., Delachapelle, H. & Decocq, G. (2007) When Oskar meets Alice: does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? *Forest Ecology and Management*, 247, 120–130.
- Dechoum, M.S., Zenni, R.D., Castellani, T.T., Zalba, S.M. & Rejmánek, M. (2015) Invasions across secondary forest successional stages: effects of local plant community, soil, litter, and herbivory on *Hovenia dulcis* seed germination and seedling establishment. *Plant Ecology*, 216, 823–833.
- Donnelly, A. & Yu, R. (2021) Temperate deciduous shrub phenology: the overlooked forest layer. *International Journal of Biometeorology*, 65, 343–355.
- Dray, S. & Josse, J. (2015) Principal component analysis with missing values: a comparative survey of methods. *Plant Ecology*, 216, 657–667.
- Elith, J., Leathwick, J. & Hastie, T.A. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802–813.
- Fridley, J.D. (2008) Of Asian forests and European fields: Eastern U.S. plant invasions in a global floristic context. *PLoS One*, 3, e3630.
- Fridley, J.D. (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, 485, 359–362.
- Fridley, J.D. (2013) Plant invasions across the Northern Hemisphere: a deep-time perspective. *Annals of the New York Academy of Sciences*, 1293, 8–17.
- Fridley, J.D. & Craddock, A. (2015) Contrasting growth phenology of native and invasive forest shrubs mediated by genome size. *New Phytologist*, 207, 659–668.
- Funk, J.L. (2013) The physiology of invasive plants in low-resource environments. *Conservation Physiology*, 1, cot026.
- Funk, J.L., Parker, I.M., Matzek, V., Flory, S.L., Aschehoug, E.T., D'Antonio, C.M. et al. (2020) Keys to enhancing the value of invasion ecology research for management. *Biological Invasions*, 22, 2431–2445.
- Funk, J.L. & Vitousek, P.M. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446, 1079–1081.
- Gallinat, A.S., Primack, R.B. & Wagner, D.L. (2015) Autumn, the neglected season in climate change research. *Trends in Ecology & Evolution*, 30, 169–176.
- Givnish, T.J. (2002) Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, 36, 703–743.
- Greenberg, C.H., Smith, L.M. & Levey, D.J. (2001) Fruit fate, seed germination and growth of an invasive vine—an experimental test of 'sit and wait' strategy. *Biological Invasions*, 3, 363–372.
- Greenwell, B., Boehmke, B., Cunningham, J. & GBM Developers. (2019) gbm: generalized boosted regression models (R package version 2.1).
- Grime, J.P. (2006) *Plant strategies, vegetation processes, and ecosystem properties*. Wiley.
- Grotkopp, E. & Rejmánek, M. (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, 94, 526–532.
- Guo, W.Y., van Kleunen, M., Winter, M., Weigelt, P., Stein, A., Pierce, S. et al. (2018) The role of adaptive strategies in plant naturalization. *Ecology Letters*, 21, 1380–1389.
- Hallik, L., Niinemets, Ü. & Wright, I.J. (2009) Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *New Phytologist*, 184, 257–274.
- Harrington, R.A., Brown, B.J. & Reich, P.B. (1989) Ecophysiology of exotic and native shrubs in Southern Wisconsin. *Oecologia*, 80, 356–367.
- Heberling, J.M. & Fridley, J.D. (2016) Invaders do not require high resource levels to maintain physiological advantages in a temperate deciduous forest. *Ecology*, 97, 874–884.
- Heberling, J.M., Kichey, T., Decocq, G. & Fridley, J.D. (2016) Plant functional shifts in the invaded range: a test with reciprocal forest invaders of Europe and North America. *Functional Ecology*, 30, 875–884.
- Herron, P.M., Martine, C.T., Latimer, A.M. & Leicht-Young, S.A. (2007) Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Diversity and Distributions*, 13, 633–644.
- Hijmans, R.J., Phillips, S., Leathwick, & Elith, J. (2017) dismo: species distribution modelling. R package version 1.1–4.
- Hinman, E.D. & Fridley, J.D. (2018) To spend or to save? Assessing energetic growth-storage tradeoffs in native and invasive woody plants. *Oecologia*, 188, 659–669.
- Hoyos, L.E., Gaviera-Pizarro, G.I., Kuemmerle, T., Bucher, E.H., Radeloff, V.C. & Tecco, P.A. (2010) Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Córdoba, Argentina. *Biological Invasions*, 12, 3261–3275.
- Huston, M. (1993) Biological diversity, soils, and economics. *Science*, 262, 1676–1680.
- Jo, I., Fridley, J.D. & Frank, D.A. (2015) Linking above- and below-ground resource use strategies for native and invasive species of temperate deciduous forests. *Biological Invasions*, 17, 1545–1554.
- Jo, I., Fridley, J.D. & Frank, D.A. (2016) More of the same? In situ leaf and root decomposition rates do not vary between 80 native and non-native deciduous forest species. *New Phytologist*, 209, 115–122.
- Jo, I., Fridley, J.D. & Frank, D.A. (2017) Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *Journal of Ecology*, 105, 1105–1110.
- Kim, Y.D., Kim, S.H. & Landrum, L.R. (2004) Taxonomic and phylogeographic implications from ITS phylogeny in *Berberis* (Berberidaceae). *Journal of Plant Research*, 117, 175–182.
- Křivánek, M. & Pyšek, P. (2006) Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe). *Diversity Distributions*, 12, 319–327.
- Larrue, S., Daehler, C., Vautier, F. & Bufford, J.L. (2014) Forest invasion by the African tulip tree (*Spathodea campanulata*) in the Hawaiian Islands: are seedlings shade-tolerant? *Pacific Science*, 68, 345–358.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545–556.
- Lieurance, D. & Cipollini, D. (2013) Exotic *Lonicera* species both escape and resist specialist and generalist herbivores in the introduced range in North America. *Biological Invasions*, 15, 1713–1724.

- Lechowicz, M.J. (1984) Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *The American Naturalist*, 124, 821–842.
- Linderholm, H.W. (2006) Growing season changes in the last century. *Agricultural and Forest Meteorology*, 137, 1–14.
- Loh, R.K. & Daehler, C.C. (2007) Influence of invasive tree kill rates on native and invasive plant establishment in a Hawaiian forest. *Restoration Ecology*, 15, 199–211.
- Lopez, O.R., Farris-Lopez, K., Montgomery, R.A. & Givnish, T.J. (2008) Leaf phenology in relation to canopy closure in southern Appalachian trees. *American Journal of Botany*, 95, 1395–1407.
- Major, K.C., Nosko, P., Kuehne, C., Campbell, D. & Bauhus, D.J. (2013) Regeneration dynamics of non-native northern red oak (*Quercus rubra* L.) populations as influenced by environmental factors: a case study in managed hardwood forests of southwestern Germany. *Forest Ecology and Management*, 291, 144–153.
- Martin, P.H., Canham, C.D. & Kobe, R.K. (2010) Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. *Journal of Ecology*, 98, 778–789.
- Martin, P.H., Canham, C.D. & Marks, P.L. (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment*, 7, 142–149.
- Martinez, K.A. & Fridley, J.D. (2018) Acclimation of leaf traits in seasonal light environments: are non-native species more plastic? *Journal of Ecology*, 106, 2019–2030.
- Meyer, J.Y. & Florence, J. (1996) Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). *Journal of Biogeography*, 23, 775–781.
- Morris, L.L., Walck, J.L. & Hidayati, S.N. (2002) Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): implications for the invasion and persistence of a nonnative shrub. *International Journal of Plant Sciences*, 163, 1001–1010.
- Moles, A.T., Flores-Moreno, H., Bonser, S.C., Warton, D.I., Helm, A. & Warman, L. et al. (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, 100, 116–127.
- Mulder, C.P. & Spellman, K.V. (2019) Do longer growing seasons give introduced plants an advantage over native plants in Interior Alaska? *Botany–Botanique*, 97, 347–362.
- Müller-Schärer, H., Schaffner, U. & Steinger, T. (2004) Evolution in invasive plants: implications for biological control. *Trends in Ecology & Evolution*, 19, 417–422.
- Novoa, A., Richardson, D.M., Pyšek, P., Meyerson, L.A., Bacher, S., Canavan, S. et al. (2020) Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, 22, 1801–1820.
- O'Connell, E. & Savage, J. (2020) Extended leaf phenology has limited benefits for invasive species growing at northern latitudes. *Biological Invasions*, 22, 2957–2974.
- Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B. et al. (2019) vegan: community ecology package. R package version 2.5-6.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs*, 66, 1–43.
- Palter, J.B. (2015) The role of the Gulf Stream in European climate. *Annual Review of Marine Science*, 7, 113–137.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2020) nlme: linear and nonlinear mixed effects models. R package version 3.1–144.
- Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, 87, 1733–1743.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. et al. (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, 89, 1908–1920.
- Pyšek, P. & Richardson, D.W. (2007) Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.) *Biological invasions*. Berlin: Springer, pp. 97–126.
- R Core Team. (2020) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org>
- Rehder, A. (1940) *Manual of cultivated trees and shrubs hardy in North America: exclusive of the subtropical and warmer temperate regions*. New York, NY: MacMillan.
- Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, 102, 275–301.
- Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conservation Biology*, 11, 193–203.
- Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plants species more invasive? *Ecology*, 77, 1655–1661.
- Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.
- Schierenbeck, K.A., Mack, R.N. & Sharitz, R.R. (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology*, 75, 1661–1672.
- Shouman, S., Mason, N.W.H., Kichey, T., Closset-Kopp, D., Heberling, M., Kobeissi, A. et al. (2017) Functional shift of sycamore maple (*Acer pseudoplatanus*) towards greater plasticity and shade tolerance in its invasive range. *Perspectives in Plant Ecology Evolution and Systematics*, 29, 30–40.
- Stacklies, W., Redestig, J., Scholz, M., Walther, D. & Selbig, J. (2007) pcaMethods—a bioconductor package providing PCA methods for incomplete data. *Bioinformatics*, 23, 1164–1167.
- Suda, J., Meyerson, L.A., Leitch, I.J. & Pyšek, P. (2015) The hidden side of plant invasions: the role of genome size. *New Phytologist*, 205, 994–1007.
- USDA, NRCS. (2020) *The PLANTS database (national plant data team)*. <http://plants.usda.gov>
- van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13, 235–245.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L. et al. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708.
- Webster, C.R., Jenkins, M.A. & Jose, S. (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *Journal of Forestry*, 104, 366–374.
- Wolkovich, E.M., Davies, T.J., Schaefer, H., Cleland, E.E., Cook, B.I. & Travers, S.E. (2013) Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany*, 100, 1407–1421.
- Xu, C.Y., Griffin, K.L. & Schuster, W.S.F. (2007) 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.
- Yamashita, N., Tanaka, N., Hoshi, Y., Kushima, H. & Kamo, K. (2003) Seed and seedling demography of invasive and native trees of subtropical Pacific islands. *Journal of Vegetation Science*, 14, 15–24.
- Yin, J., Fridley, J.D., Smith, M. & Bauerle, T. (2015) Xylem vessel traits predict the leaf phenology of native and non-native understory species of temperate deciduous forests. *Functional Ecology*, 30, 206–214.
- Zohner, C.M., Benito, B., Fridley, J.D., Svenning, J.-C. & Renner, S. (2017) Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe, and East Asia. *Ecology Letters*, 20, 452–460.

Zohner, C.M. & Renner, S.S. (2017) Innately shorter vegetation periods in North American species explain native–non-native phenological asymmetries. *Nature Ecology and Evolution*, 1, 1655–1660.

### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**How to cite this article:** Fridley, J.D., Bauerle, T.L., Craddock, A., Ebert, A.R., Frank, D.A., Heberling, J.M., et al. (2022) Fast but steady: An integrated leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters*, 25, 900–912.  
Available from: <https://doi.org/10.1111/ele.13967>