REVIEW

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

A general hypothesis of forest invasions by woody plants based on whole-plant carbon economics

Jason D. Fridley[1] | Peter J. Bellingham[2,3] | Déborah Closset-Kopp[4] |
Curtis C. Daehler[5] | Michele S. Dechoum[6] | Patrick H. Martin[7] | Helen T. Murphy[8] |
Julissa Rojas-Sandoval[9] | David Tng[10]

[1]Department of Biology, Syracuse University, Syracuse, New York, USA; [2]Manaaki Whenua – Landcare Research, Lincoln, New Zealand; [3]School of Biological Sciences, University of Auckland, Auckland, New Zealand; [4]Unité Ecologie et Dynamique des Systèmes Anthropisés, University of Picardie Jules Verne, Amiens, France; [5]School of Life Sciences, University of Hawai'i at Mānoa, Honolulu, Hawaii, USA; [6]Departamento de Ecologia e Zoologia, Programa de Pós-Graduação em Ecologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil; [7]Department of Biological Sciences, University of Denver, Denver, Colorado, USA; [8]CSIRO, Townsville, Queensland, Australia; [9]Institute of the Environment, University of Connecticut, Storrs, Connecticut, USA and [10]Centre for Rainforest Studies, The School for Field Studies, Yungaburra, Queensland, Australia

Correspondence
Jason D. Fridley
Email: fridley@clemson.edu

Present address
Jason D. Fridley, Department of Biological Sciences, Clemson University, Clemson, South Carolina, USA

Funding information
National Science Foundation, Grant/Award Number: IOS-1754273; New Zealand Ministry of Business, Innovation and Employment

Handling Editor: Ayub Oduor

Abstract

1. Although closed-canopy forests are characterized by low-light availability and slow population dynamics, many are under threat from non-native, invasive woody species that combine high colonization ability and fast growth potential with high low-light survival. This 'superinvader' phenotype contravenes expected trade-offs predicted by successional niche theory, posing a challenge to both invasion and forest succession theory.

2. We propose a parsimonious conceptual model based on the whole-plant light compensation point (WPLCP) that, across a variety of plant strategies and growth forms, can explain greater competitive abilities of forest invaders in the context of both high-light growth rate and shade tolerance. The model requires only that non-native species experience relatively fewer carbon costs than native species, enabling resource-acquisitive species to establish in low-light conditions.

3. We review evidence for lower carbon costs in invasive species resulting from (1) enemy release, (2) recent environmental changes that favour less stress-tolerant phenotypes and (3) phylogenetically constrained native floras. We also discuss implications of invader shade tolerance in the context of other life-history strategies that, combined with canopy disturbances, facilitate their rapid numerical dominance.

4. *Synthesis.* An invasion framework driven by carbon dynamics suggests renewed focus on whole-plant carbon costs, including below-ground respiration and tissue turnover, which are rarely measured in functional studies of forest invaders.

1 | INTRODUCTION

Invasions of closed-canopy forests by shade-tolerant plants are a growing conservation concern (Martin et al., 2009; Medvecká et al., 2018; Rejmánek, 2014; Webster et al., 2006) and pose several challenges to existing concepts of community invasibility and attributes of invasive species (Fridley et al., 2022; Funk, 2013; Martin et al., 2009). For example, although disturbances are an important driver of forest population dynamics (Pacala et al., 1996) and disturbance has long played a central role in theories of invasion (Fox & Fox, 1986), closed-canopy forests are characterized by low-light availability and slow population dynamics that, in the absence of disturbance, are thought to limit opportunities for invasion (Davis et al., 2000; Rejmánek, 1996; Von Holle et al., 2003). In addition, comparative functional studies of native and invasive species often indicate invaders are biased towards a fast life history and traits that promote rapid resource acquisition (e.g. Guo et al., 2018; Montesinos, 2022; Rejmanek & Richardson, 1996; van Kleunen et al., 2010). These traits, which seem to be common in forest invaders, confer high growth capacity, a fitness advantage in disturbed habitats but generally thought to be selected against in closed-canopy conditions (Hallik et al., 2009; Poorter et al., 2008). Yet invasions of closed-canopy forests are common: Martin et al. (2009) listed over 130 examples of shade-tolerant invaders across temperate and tropical forested biomes, calling into question the idea that resource availability per se is predictive of community invasibility (Davis et al., 2000; Levine et al., 2004). Thus, existing invasion and succession theories seem deficient in predicting which forests are most invasible and by which species, a situation that continues to stymie the application of invasion research to management (Funk et al., 2020).

Forest invasions by woody plants are also exceptional in the context of adaptive trade-off theory (Agrawal, 2020). Among native species, light partitioning is among the most well-established examples of ecological specialization in woody plants: shade-tolerant species have traits that minimize tissue respiration and turnover, and thus the whole-plant light compensation point (WPLCP, the light level at which net growth is zero; Givnish, 1988; Lusk & Jorgensen, 2013; Walters & Reich, 2000); these same traits prevent rapid growth and competitive dominance in high-light conditions (Kobe et al., 1995; Sendall et al., 2016). To establish and persist in closed-canopy forests, a non-native species requires some tolerance of low-light conditions, but trade-off theory expects low-resource tolerance should come at the expense of competitive abilities in high-resource conditions. However, there is a particular class of woody invaders in both temperate and tropical forests that appear to defy this key trade-off. These 'superinvaders' (Table 1; based on the 'superspecies' phenotype of Pacala et al., 1996) grow faster than most or all co-occurring native species when light is abundant, yet establish and/or persist in shade, thus outcompeting native species across disturbance gradients (Bellingham et al., 2018; Herron et al., 2007; Martin et al., 2010; Yamashita et al., 2003). Many of these species also have high reproductive allocation (Martin & Canham, 2010) and mature at smaller

size classes than natives (Table 1). A conceptual framework that could explain how forest superinvaders express this combination of fast growth, shade tolerance and high fecundity would facilitate forest invader risk assessment and further mechanistic understanding of both plant invasions and forest succession (Davis et al., 2001; Pacala et al., 1996).

Here, we summarize what is known about woody forest invaders in temperate and tropical habitats and identify functional and life-history traits that suggest a common forest superinvader phenotype. In summarizing the current understanding of shade tolerance adaptations in woody plants, we propose a conceptual framework based on understory carbon dynamics that explains how these invaders can simultaneously express faster growth and similar shade tolerance compared with native species, emphasizing the role of carbon costs in driving both growth rate and WPLCP, a strong driver of species survival in shade (Baltzer & Thomas, 2007a; Lusk & Jorgensen, 2013). Although measurements of whole-plant carbon budgets along light gradients are scarce in invasion research, we review several well-known invasion mechanisms that could lead to lower carbon costs for forest invaders than co-occurring native species. Because shade tolerance is predominantly a mechanism that enables species to persist during low-light conditions until canopy disturbances free up resources for growth and reproduction, we consider the superinvader phenotype in the context of gap-phase dynamics to explain how the combination of fast life-history traits (Reich, 2014) and high shade tolerance may be the key to understanding forest dominance by invasive species.

Throughout, we define closed-canopy forests as those sufficiently mesic to support high densities of large trees. Closed-canopy forests have high leaf area indices and low light in the understorey at peak growing season. Once canopy closure occurs, variation in light becomes the key limiting resource across forest types globally, whether tropical, temperate, boreal, lowland or montane (Canham et al., 1990). In such conditions, the low-light adaptations of plant species are paramount; variation in other resources, such as soil fertility, can modify the effects of shading (i.e. resource colimitation; e.g. Martin & Marks, 2006), but these typically play a secondary role in all but extreme cases of nutrient limitation (Coomes & Grubb, 2000).

2 | TRAITS OF FOREST SUPERINVADERS

Martin et al. (2009) listed 139 species of shade-tolerant invasive plants, including herbaceous species. We focus on woody invaders because studies of adaptive trade-offs along light gradients are best understood for woody plants; for ease of ecological comparison, we further limit our focus to tree and shrub growth habits, excluding groundcovers, subshrubs (e.g. *Lantana camara*), scramblers (e.g. *Rosa* spp.), climbers and vines. Shrubs and trees account for 68 species on the Martin et al. (2009) list. Most of these are little studied and their ecological traits largely unknown. We selected 20 species (Table 1, Plate 1) that are relatively well represented in the literature and are

TABLE 1 Woody forest 'superinvaders' that grow quickly in high light, establish and/or persist beneath a closed canopy and have high fecundity. This is a selection of well-documented trees and shrubs; herbs, groundcovers, subshrubs, scramblers, climbers and vines are excluded. Maximum growth rate refers to behaviour in the invaded range

Species	Invaded locations	Native range	Max growth rate	Establishes in shade?	Persists after canopy closure?	Fecundity	Stature	References
Temperate forests								
Acer platanoides	North America	Europe	High	Yes	Yes	High	Tall tree	Martin (1999); Martin et al. (2010); Niinemets (1998); Wyckoff and Webb (1996)
Berberis thunbergii	North America	East Asia	High	Yes	Yes	High	Shrub	Silander and Klepeis (1999); Heberling and Fridley (2013)
Elaeagnus umbellata	North America	East Asia	High	Yes	Yes	High	Shrub	Edgin and Ebinger (2001); Soley and Sipes (2021)
Ligustrum lucidum	South America, Australia, NZ, North America	East Asia	High	Yes	Yes	High	Small tree	Aguirre-Acosta et al. (2014); Easdale and Healey (2009); Hoyos et al. (2010); Fernandez et al. (2020, 2021)
Ligustrum sinense	Argentina, North America, Australia, New Zealand	East Asia	High	Yes	Yes	High	Small tree	Grove and Clarkson (2005); Loewenstein and Loewenstein (2005); Morris et al. (2002)
Lonicera maackii	North America	East Asia	High	Yes	Yes	High	Shrub	Hartman and McCarthy (2008); Lieurance and Landsbergen (2016); Luken and Goessling (1995); Luken and Thieret (1996); Luken et al. (1997)
Prunus serotina	Europe	North America	High	Yes	Yes	High	Tall tree	Closset-Kopp et al. (2007); Vanhellemont et al. (2011)
Quercus rubra	Europe	North America	High	Yes	Yes	Moderate	Tall tree	Kuehne et al. (2014); Major et al. (2013); Woziwoda et al. (2014)
Rhamnus cathartica	North America	Europe, Central Asia	High	Yes	Yes	High	Small tree	Knight et al. (2007); Qaderi et al. (2009); Schuster et al. (2020); Heberling et al. (2016)
Triadica sebifera[a]	North America	Australia, East Asia	High	Yes	Yes	High	Small tree	Butterfield et al. (2004); Jones and McLeod (1989); Jubinsky and Anderson (1996)
Tropical and subtropical forests								
Ardisia elliptica	Caribbean, Florida, Hawaii	Australia, Southeast Asia	High	Yes	Yes	High	Small tree	Horvitz et al. (1998); Pascarella and Horvitz (1999); Zhao and Chen (2011)
Bischofia javanica	Subtropical Japan, Florida	Asia, Australia, Micronesia	High	Yes	Yes	High	Tall tree	Hata et al. (2006); Yamashita et al. (2000, 2002, 2003)
Hovenia dulcis	Brazil	East Asia	High	Yes	Yes	High	Small tree	Carvalho (1994); Dechoum et al. (2015)
Miconia crenata[b]	Tropics (widespread)	Central, South America	High	Yes	Yes	High	Shrub	DeWalt (2006); DeWalt et al. (2004); Waddell et al. (2020)

(Continues)

TABLE 1 (Continued)

Species	Invaded locations	Native range	Max growth rate	Establishes in shade?	Persists after canopy closure?	Fecundity	Stature	References
Miconia calvescens	Tropics (widespread)	Central, South America	High	Yes	Yes	High	Small tree	Meyer and Florence (1996); Meyer (1997); Baruch et al. (2000)
Pittosporum undulatum	Jamaica, Azores, South Africa	Australia	High	Yes	Yes	Moderate	Small tree	Ball (2000); Bellingham et al. (2005, 2018); Chai et al. (2012); Goodland and Healey (1996)
Psidium cattleyanum	Tropics (widespread)	South America	High	Yes	Yes	High	Small tree	Florens et al. (2016); Huenneke and Vitousek (1990); Landrum (2017); Tng et al. (2016)
Spathodea campanulata	Hawaii, Puerto Rico, Tahiti	Africa, Australia	High	Yes	Yes	High	Tall tree	Larrue et al. (2015); Lugo (2004)
Sphaeropteris cooperi[c]	Hawaii, New Zealand, Mauritius	Australia	High	Yes	Yes	High	Small tree	Durand and Goldstein (2001); Medeiros et al. (1992)
Syzygium jambos	Tropics (widespread)	Southeast Asia	Moderate	Yes	Yes	Moderate	Small tree	Brown et al. (2006); Pascarella et al. (2000); Thompson et al. (2007); Martin et al. (2004)

[a]Synonym *Sapium sebiferum*.
[b]Synonym *Clidemia hirta*.
[c]Synonym *Cyathea cooperi*.

frequent targets of eradication or control in forested regions, split equally between temperate and tropical biomes. Woody invaders of boreal forests are rare (but see Nestby, 2020), likely due to the circumboreal distribution of many native species, lack of such forests in the Southern Hemisphere and low introduction effort.

Tropical forest superinvaders are often widely distributed and are seen as primary threats to native biodiversity, particularly in Australia and across islands in the Pacific and Caribbean. *Miconia calvescens*, *Miconia crenata* (syn. *Clidemia hirta*), *Pittosporum undulatum*, *Psidium cattleyanum*, *Spathodea campanulata* and *Syzygium jambos* are all widespread invasive tropical trees characterized by rapid growth and the ability to establish as seedlings beneath native forest canopies (Table 1). Those of more restricted distribution include *Bischofia javanica*, well studied in subtropical Japan (Yamashita et al., 2000, 2002), *Ardisia elliptica* in the New World tropics and Pacific, the deciduous invader *Hovenia dulcis* in subtropical Brazil and the tree fern *Sphaeropteris cooperi* (syn. *Cyathea cooperi*) across the Pacific. Most of these species produce copious seed (or spores) in comparison with co-occurring native species. Interestingly, some are uncommon in forests in their native range, including *M. crenata* (DeWalt et al., 2004), *M. calvescens* (Meyer, 1997) and *S. cooperi* (Medeiros et al., 1992).

Temperate forests are increasingly dominated by deciduous and semi-evergreen invaders in many regions, particularly in North and South America (Fridley et al., 2022; Rejmánek, 2014). *Ligustrum lucidum* and *L. sinense* are widespread globally, the former particularly dominant in South America (Fernandez et al., 2020). In North America, more than 20 non-native shrubs and small trees are commonly found in native deciduous forests (Fridley, 2008; Fridley et al., 2022), with *Lonicera maackii* dominant in central North American forests, *Rhamnus cathartica* dominant across northern hardwood forests, *Berberis thunbergii* and other shrubs in the genus *Lonicera* common in the Northeast and the N_2-fixing *Elaeagnus umbellata* abundant in warmer regions. *R. cathartica*, one of the first North American woody introductions of the European colonial period, has become the most abundant understorey tree in parts of its invaded range; in its native European range it is a forest edge species and largely absent from shady forest interiors (Kurylo et al., 2007). Although many other invasive shrubs are present in North American forests, all of the above species combine fast growth rate with tolerance of low (<10%) light levels (Table 1). In addition, *Triadica sebifera* (syn. *Sapium sebiferum*) is a common small tree invading lowland forests of southeastern North America and the tree *Acer platanoides* is a common forest invader in northern regions; there is abundant evidence that both species can outcompete natives in sun and shade (Table 1). In forests of central Europe, the North American trees *Prunus serotina* and *Quercus rubra* are locally dominant in both natural and managed forests (Closset-Kopp et al., 2007; Major et al., 2013). In contrast, there are rather few known shade-tolerant woody invaders across forests of temperate Asia, which is the largest source of temperate forest invaders elsewhere (Fridley, 2013; Heberling et al., 2017; Rejmánek, 2014).

Additional forest invaders have similar attributes as those listed in Table 1, but fewer studies have been published on them.

PLATE 1 Examples of woody superinvaders of closed-canopy forests. (a) Invasion of evergreen rain forests of the Ogasawara Islands (Japan) by *Bischofia javanica* (photo: Hiroko Kurokawa). (b) Invasion of deciduous forest in the Northeast USA by *Acer platanoides* (photo: Patrick Martin). (c) Invasion of tropical rainforest in Northeast Australia by *Miconia calvescens* (photo: Helen Murphy). (d) Invasion of subtropical deciduous forest in Southeast Brazil by *Hovenia dulcis* (light coloured canopies; photo: Michele Dechoum). (e) Invasion of deciduous forest in the Northeast USA by the shrub *Berberis thunbergii* (photo: Jason Fridley). (f) Invasion of *Psidium cattleyanum* in tropical forest in Australia (photo: David Tng). (g) Monospecific stand (adults and seedlings) of *Prunus serotina* in a nature reserve in northern France (photo: Guillaume Decocq). (h) Seedlings of *Pittosporum undulatum* in the understory of a Jamaican montane rain forest (photo: Peter Bellingham).

For example, several *Schefflera* spp. are well-known invasive trees of tropical and subtropical forests, although often establishing as epiphytes (Marciniak et al., 2020). Other potential forest superinvaders include shade-tolerant palms (*Archontophoenix cunninghamiana*, *Trachycarpus fortunei*) and other less-researched species of *Ardisia*, *Artocarpus*, *Ligustrum*, *Lonicera*, *Prunus*, *Psidium*, *Rhamnus* and *Terminalia*. Nonetheless, our compilation (Table 1) indicates that many of the most widespread and impactful woody forest invaders combine fast growth rate in high light and high survivorship in low light to an exceptional degree vis-à-vis native species (Baltzer & Thomas, 2007a; Lusk et al., 2015; Sendall et al., 2016). Is there a general explanation for this superinvader phenotype?

3 | A HYPOTHESIS OF FOREST INVASIONS BASED ON CARBON DYNAMICS

There is a large body of research documenting traits conferring shade tolerance in woody species (Valladares & Niinemets, 2008). Although many authors have made a distinction between traits related to 'defence and storage' (Kitajima, 1994; Kobe, 1997; Niinemets, 2006; Petrovska et al., 2021) versus those conferring positive net growth in shade ('carbon gain hypothesis'; Lusk & Jorgensen, 2013), all plants in the forest understorey must simultaneously avoid herbivory and environmental stress while continuing to gain stature to capture sufficient light energy to support eventual reproduction (Canham, 1985; Givnish, 1988; Pacala et al., 1996).

Thus, although specific adaptive strategies in shade will vary – depending on rates and sizes of gap formation, the frequency of large disturbances, rates of herbivory and costs of nutrient uptake, among other factors – the process of forest invasion is initially driven by light availability and the need to minimize energy expenditures in the face of extreme light scarcity, even if for relatively short time periods. Consistent with this view is strong empirical evidence supporting net carbon gain as the primary driver of sapling survival in shade (Baltzer & Thomas, 2007a; King, 1994; Lusk et al., 2015; Lusk & Jorgensen, 2013; Sendall et al., 2016; Walters & Reich, 2000).

We develop the idea of light availability and net carbon (C) gain as a dominant factor driving forest invasions using the concept of WPLCP (Givnish, 1988). WPLCP is the light level at which C gain balances whole-plant C losses from tissue respiration (including maintenance and growth) and turnover (including shedding and loss from disturbance and herbivory; Figure 1a). Individuals cannot survive in light conditions below their WLPCP over long periods because they would have insufficient energy to support their metabolism (Pacala et al., 1996). For example, taller woody plants experience greater relative C costs due to greater wood investment per unit leaf mass (Falster et al., 2018), thus increasing their WPLCP for a given leaf-level C gain curve and increasing their light requirements for positive growth. Similarly, species experiencing greater tissue loss from herbivory have reduced shade tolerance due to an increase in WPLCP (Lusk & Jorgensen, 2013). Larger C investments in below-ground tissues and functions (e.g. fine roots, exudates, microbial mutualisms) and defensive structures (e.g. thorns) or chemicals (e.g. phenols, lignin) predict similar reductions in shade tolerance. Reproductive individuals face additional energetic costs, including the development of flowers and fruits (Fridley, 2017), which should further increase WPLCP at the time of reproduction. Thus, immature saplings should be more shade-tolerant than mature individuals producing seed (Figure 1a).

If shade tolerance is driven by an individual's ability to maintain positive net C balance at low-light levels, then any reduction in C costs – for example, removal of an herbivore – will lead to greater shade tolerance. We hypothesize that non-native species that become invasive in forests have lower C costs than native species, regardless of potential differences in gross photosynthetic rate. Moreover, a reduction in C costs for an individual will also increase its growth rate in high light because relative growth rate is the difference between C gain and C loss at the whole-plant level. We demonstrate this conceptually in Figure 1b. Lower C costs can come from several mechanisms, including reduced herbivory or defence investment, longer tissue life span, fewer support structures, shorter stature, reduced below-ground investment or less investment in adaptations that confer resistance to other stresses (e.g. drought, freezing). We propose this relationship between C costs, shade tolerance and growth rate as a parsimonious explanation for the forest superinvader phenotype, under the single assumption that these invaders experience fewer C costs. This net C gain advantage increases the competitive ability of invaders across the light gradient, without invoking other competitive mechanisms, such as the production of allelopathic compounds (Zhang et al., 2021), denser growth or shading (Wyckoff & Webb, 1996) or greater apparent quantum yield (Heberling & Fridley, 2016) that may further contribute to invader dominance in some ecosystems.

A key prediction of this net C gain hypothesis of forest invasions is that a reduction in C costs will allow more acquisitive species to persist at lower light levels than they otherwise could (Figure 1c). That is, if a non-native plant experiences lower C costs in its invaded range, it could inhabit shadier locations than in its native range – even if it otherwise expressed 'fast' traits associated with high growth rates. This may explain why many forest invaders have leaf traits of greater N content and maximum photosynthetic rate (A_{sat}) than native species (Fridley et al., 2022). For example, Heberling and Fridley (2013) demonstrated substantially larger A_{sat} for forest invaders in light curve comparisons for 32 native and invasive species of North American forests. More generally, the net C gain framework may explain what to date has been a paradox in functional trait studies of forest invaders that possess qualities of both shade-tolerant and shade-intolerant species (Closset-Kopp et al., 2007; Fridley et al., 2022; Funk, 2013; Shouman et al., 2020).

Box 1 describes a simulation that illustrates the influence of C costs on light partitioning for a set of native and invasive species differing in whole-plant C costs. We emphasize that competitive dominance by invaders in forests is rarely, if ever, simply due solely to either shade tolerance or fast growth rate – rather, because understorey light environments are dynamic over the life span of woody plants, it is the combination of shade tolerance, rapid growth potential and high fecundity that ultimately leads to numerical dominance and displacement of native species. We expand on this issue below in the context of invader life-history strategies.
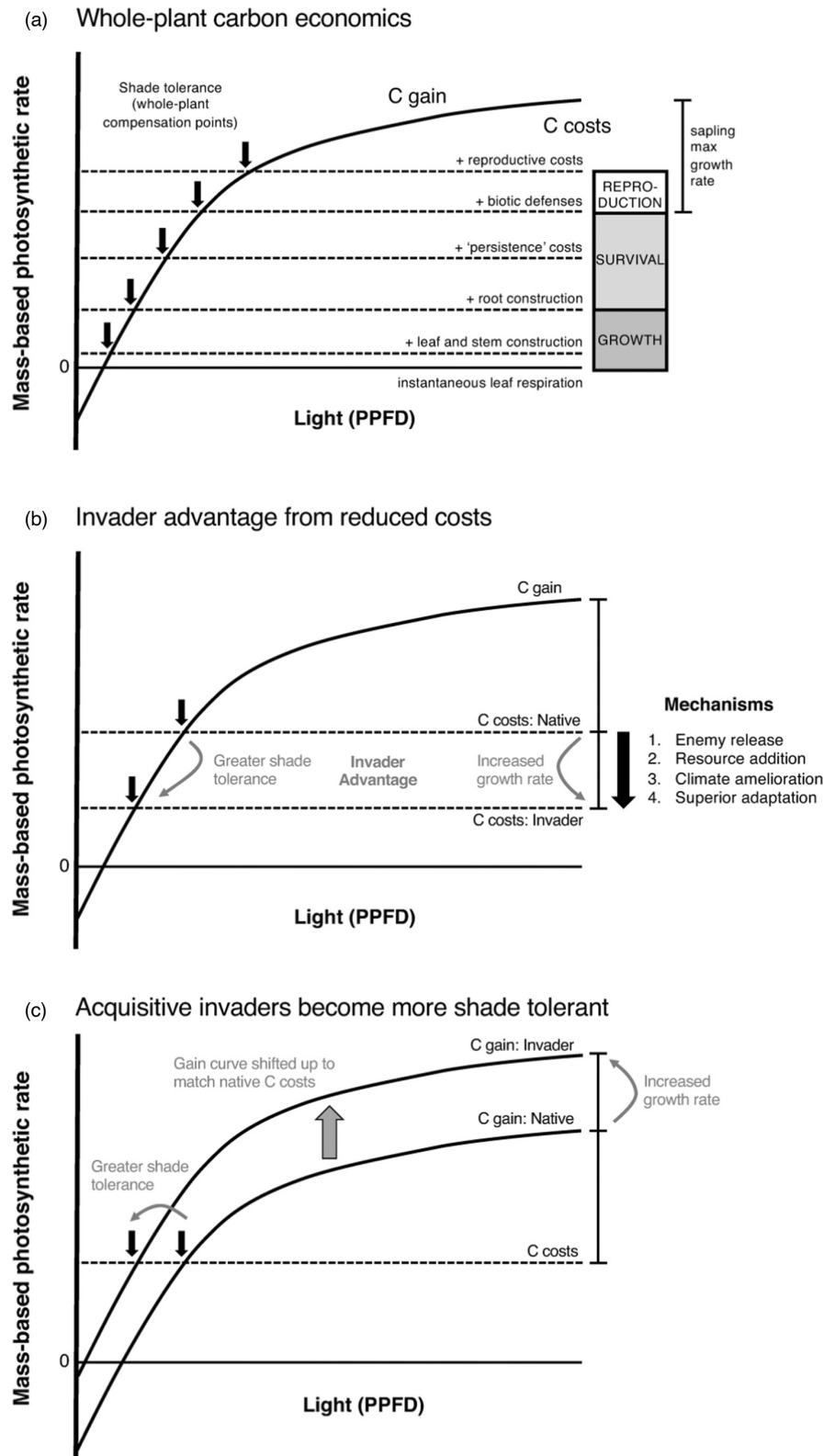
4 | MECHANISMS PROMOTING LOWER CARBON COSTS IN INVADERS

Whole-plant C costs are difficult to measure because they require capture of CO_2 fluxes above- and below-ground (Kong & Fridley, 2019) and mark/recapture techniques to estimate tissue turnover rates, both of which are expensive to monitor in the field. Thus, although some components, such as leaf dark respiration rate, are often measured in native–invader trait comparisons, measures of most aspects of C costs are not available. However, several common invasion mechanisms involve reduced C costs in invaders. We group these into (1) enemy release, including shifts away from defence allocation in the invaded range from plasticity or rapid evolution, (2) recent environmental changes that select against native species that have costly stress adaptations and (3) phylogenetic constraints of 'disharmonic' native forest floras that reduce resource uptake efficiencies compared with non-native species.

4.1 | Enemy release

Release from natural enemies can influence an invader's C balance both by decreasing the plant's losses from attack (Cincotta

FIGURE 1 (a). Whole-plant light compensation points after accounting for carbon (C) costs associated with building and maintaining leaves, stems and roots (growth costs); 'persistence' mechanisms including C storage to support resprouting, clonal reproduction and defences against predators and pathogens (survival costs); and those supporting reproduction (flowers, fruits). Modified from Figure 3 of Givnish (1988). For a given light assimilation curve (C gain), C costs influence both shade tolerance and growth rate in high light (gain minus growth and survival costs prior to reproduction). (b). Reduced C costs in invaders are predicted to increase both high-light growth rate and shade tolerance, even in the absence of photosynthetic rate differences. (c) Invaders of high photosynthetic potential may still achieve greater shade tolerance than native species if they experience similar C costs.

(a) Whole-plant carbon economics

(b) Invader advantage from reduced costs

(c) Acquisitive invaders become more shade tolerant

et al., 2009) and reducing the need for investment in C-based defences. In the context of forest invasions, these effects can increase an invader's shade tolerance, with a larger absolute change in shade tolerance and C gain potentially expected by invaders with higher A_{sat} (Figure 2). For example, enemy release explains successful invasion by *M. crenata* (syn. *C. hirta*) into shaded habitats.

In its native range, *M. crenata* individuals planted in forests rarely survived, but when they were protected from herbivores and pathogens, their survival and growth rates increased significantly in shade (DeWalt et al., 2004). In contrast, strong effects of natural enemy release were not observed in open habitats of its native range. In its invaded range, natural enemies appeared to have

BOX 1 Simulating invader advantages across a light gradient

To illustrate the impact of species differences in net C gain on forest invasions, we simulate photosynthetic light response curves for a set of native and invasive species that differ only in whole-plant C costs. In this scenario, five native species (panel A) vary in light-saturated photosynthetic rate (A_{sat}), at 1, 2, 4, 8 and 20 mmol CO_2 g^{-1} d^{-1}; following Givnish ([1988](#)), A_{sat} is expressed per unit leaf mass rather than leaf area to enable comparison with mass-based C costs. We assume leaf-level respiratory costs are proportional to A_{sat} and that species of lower metabolic rate approach A_{sat} at lower light values. This can be expressed as a Michaelis–Menten function of asymptote A_{sat} and half-saturation constant K, where K is proportional to A_{sat} (Givnish et al., [2004](#)):

$$\text{Net C Gain} = \left[(\text{PPFD} \times A_{sat}) / (\text{PPFD} + K) \right] - R.$$

Here, R is daily leaf dark respiration rate (mmol CO_2 g^{-1} d^{-1}) and PPFD is photosynthetic photon flux density (µmol photos m^{-2} s^{-1}); assuming $R = A_{sat}/10$ and $K = 75 \times A_{sat}$ leads to crossover in net C gain curves along a light gradient as shown in panel A. At the whole-plant level (panel B), we further assume C costs remain proportional to A_{sat} as a result of greater tissue turnover in species of higher metabolic rate, and use the same Michaelis–Menten function but with a larger loss rate, increasing R from $0.1 \times A_{sat}$ to $0.3 \times A_{sat}$. The rank order of high-light growth rates (net C gain at PPFD = 2000) and WPLCPs (PPFD at which net C gain = 0) remain the same, but zero growth occurs at higher light levels as a result of greater C costs for all species. Panel C shows the same native light curves as B, adding a set of invasive species (red lines) of equivalent A_{sat} and K, but with 20% less whole-plant C cost than natives ($R = 0.24 \times A_{sat}$ vs. $0.3 \times A_{sat}$). The result is that invaders have both greater high-light growth rates and lower WPLCP than native species (panel D).
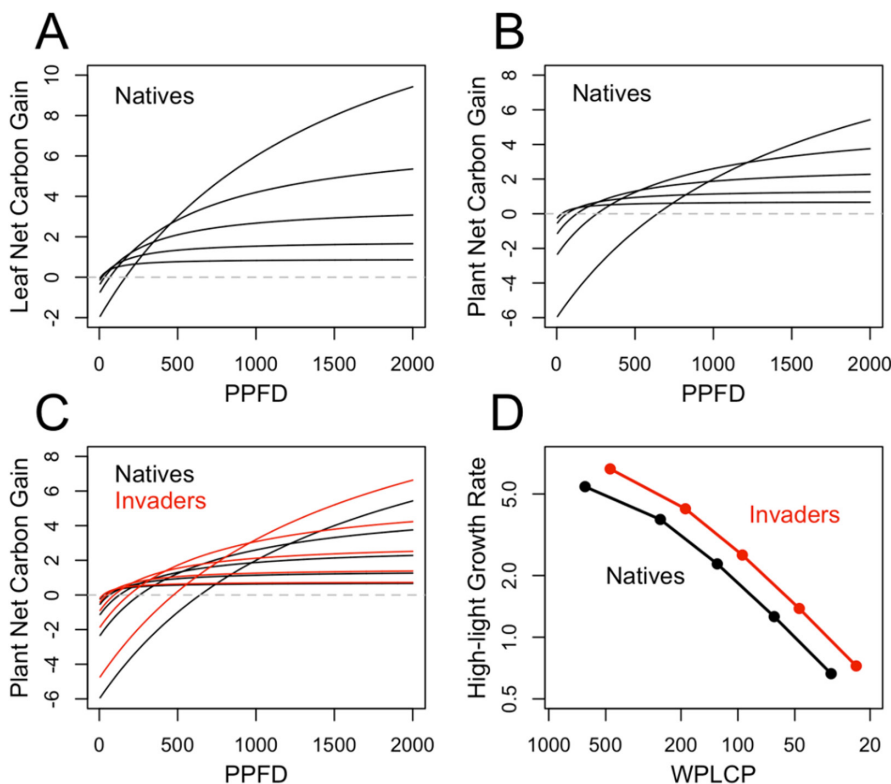
little effect on *M. crenata,* and it formed dense stands in forests (DeWalt et al., [2004](#)). A similar pattern was observed in *Toona ciliata,* a shade-intolerant tree naturalized in forests of Hawai'i. In its native range, exclusion of fungal pathogens allowed seedlings to emerge in dense shade, although pathogen exclusion did not increase long-term seedling survival (Krishnadas & Comita, [2018](#)). In the native range of invaders, specialized seedling pathogen loads

have been reported to increase with shading for some trees, such as oaks (Mutz et al., [2021](#)), and these specialized natural enemies may be left behind when plants are introduced to a new geographic range (e.g. Perkins et al., [2008](#)). For example, the superinvader *Q. rubra* showed higher seedling survival rates near parent trees than native species in Poland (Dyderski & Jagodziński, [2019](#)). Similarly, Augspurger and Kelly ([1984](#)) found that fast-growing
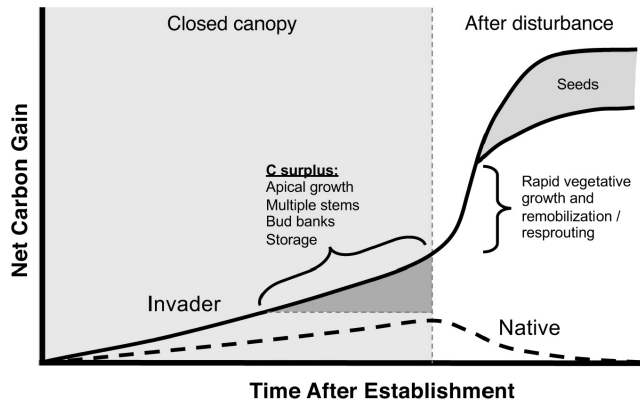
FIGURE 2 Carbon surplus (grey triangle) from lower costs enables an array of life-history strategies in invaders that permit rapid exploitation of eventual light gaps from canopy disturbance. Compared with lower net C gain of understory native saplings, invaders may invest in several strategies that prepare suppressed saplings for rapid growth and reproduction when light levels increase after disturbance, including: (1) tall stature (apical growth), enabling light usurpation; (2) clonal growth and formation of multiple stems, enabling a larger foraging area for gaps (preemptive space occupancy) and greater survival from understory disturbances (bet-hedging); (3) bud banks and C storage, supporting opportunistic sprouting and (4) C storage to facilitate stress responses after gap formation (e.g. water loss, freezing). Subsequent prolific production of small seeds at relatively small size classes is characteristic of many forest invaders that leads to rapid numerical dominance and eventual displacement of native species due to competition (decline in native curve).

species, which are typically adapted to high-light conditions at the seedling stage, tend to be more susceptible to pathogens in their native range. If fast-growing plants are particularly vulnerable to natural enemies in their native ranges, then we can expect them to exhibit relatively large increases in shade tolerance if they are released from their natural enemies (Box 1, panel C). This idea is supported by a stronger negative effect of microbial soil extracts on seedlings of species that have lower shade tolerance in their native range (McCarthy-Neumann & Kobe, 2008). We note, however, that initial invader advantages from enemy release may decay over time as invaders acquire new enemies (Diez et al., 2010; Schultheis et al., 2015) – if so, then net C gains supporting the forest superinvader phenotype may weaken and eventually reach a level consistent with native growth-survival trade-offs. We know of no empirical test of this prediction.

Although not based strictly on enemy release, facultative associations with microbial mutualists may also impact an invader's C budget relative to native species. For example, Menzel et al. (2017) showed that invasive species in Germany are less obligately mycorrhizal than native species, which may suggest reduced below-ground C allocation in support of mycorrhizal fungi. Unfortunately, there remain too few functional studies of native-invader mycorrhizal relationships to make conclusions about the role of C allocation to mycorrhizae in the superinvader phenotype (Dickie et al., 2017).

4.2 | Environmental change and stress tolerance

Plant stress adaptations typically come at a cost to overall C gain. More specifically, shade tolerance has been found to compete with tolerance of drought, extreme heat, freezing and nutrient scarcity (Baltzer & Thomas, 2007b; Craine et al., 2012; Hallik et al., 2009; Valladares et al., 1997; Walters & Reich, 2000). If the environment changes in a way that reduces the need for such stress responses, then native species may continue to express adaptations for stresses that are no longer common, thereby providing opportunities for the establishment of novel, more competitive phenotypes. In this case, some invasive woody species may have lower overall C costs in the new environment because they are less constrained by past environmental challenges than native species; such constraints may also be expressed as lower native plasticity in response to resource addition (Daehler, 2003; Pattison et al., 1998). Worldwide, forest environments are experiencing rapid changes, although not necessarily in ways that reduce the intensity of environmental stress. On the one hand, all forests have experienced a 50% increase in atmospheric CO_2 since 1800; many temperate forests have seen increases in growing season duration (Linderholm, 2006) and reductions in spring frost risk (Zohner et al., 2020); centuries of fire suppression are common in mesic temperate forests (Nowacki & Abrams, 2008); and eutrophication, particularly from atmospheric deposition, has increased nitrogen availability in some regions (Du & de Vries, 2018). If natives invest more in stress- and scarcity-relieving adaptations that are no longer necessary, they will be at a disadvantage relative to an invader that does not invest in such adaptations (Pintó-Marijuan & Munné-Bosch, 2013). In a meta-analysis across life forms and habitats, Liu et al. (2017) showed that elevated temperature and CO_2 increased the performance of invaders more than native plants. They also showed that invaders had stronger positive responses to increased N deposition and precipitation than natives and stronger negative responses to decreased precipitation. These patterns are consistent with the hypothesis that invaders in general bear fewer stress-specific adaptations and are thus more responsive to resource addition than native species.

On the other hand, climate change has increased the frequency and intensity of drought in many forested regions (Jolly et al., 2015), and some studies suggest at least some forest invaders are able to tolerate drought as well or better than native species. For example, the invader *P. cattleyanum* appears to be more drought-tolerant than several native trees on the Ogasawara Islands in Japan (Yazaki et al., 2010), and the invasive shrub *E. umbellata* in North America has high drought tolerance due to leaf trichomes that limit the damaging effects of excess radiation (Naumann et al., 2010). In secondary forests of the Seychelles, Schumacher et al. (2008) found a tendency of woody invaders to alter root allocation in response to water deficits, although drought-tolerance differences between natives and invaders were minor. Overall, while studies indicate invasive species in general show larger growth responses to resource addition at the cost of tolerance of resource scarcity, the pattern is better established for nutrients and CO_2 than for water.

Environmental change and enemy release can also interact to increase C costs for native species relative to invaders, if the abundance or consumption rates of native specialized pests and pathogens are increasing. For example, some pests of native trees are becoming larger sources of canopy disturbance because they benefit from warming temperatures (Ramsfield et al., 2016); those species that avoid such increases in consumption due to enemy release will be increasingly favoured in competition. Furthermore, human-caused extermination of top predators in forests has allowed large increases in the abundance of grazing herbivores, such as deer, leading to changes in forest understorey structure and light availability (Stromayer & Warren, 1997), which can accelerate invasion by unpalatable forest invaders such as *B. thunbergii* in North America (Link et al., 2018). Loss of predators has also increased populations of small granivores in many forests that may preferentially feed on native seeds (Galetti et al., 2015).

4.3 | Disharmonic native floras

Non-native species may be predisposed to invade native forests in regions where phylogenetic constraints have limited the evolution of ecological specialization along light gradients. In particular, oceanic island floras like those of the Hawaiian archipelago may be 'disharmonic' (Carlquist, 1974) – that is, depauperate in lineages that play important functional roles in mainland ecosystems. Drake and Mueller-Dombois (1993) and Ostertag et al. (2009) applied this concept specifically to light gradients, suggesting that montane rain forests in Hawai'i lack the large native trees that replace pioneers in more diverse continental forests, allowing the native *Metrosideros polymorpha* to dominate in both early- and late-successional stands. Similarly, Denslow (2003) and Meyer (2004) suggested that dispersal filters associated with oceanic dispersal have deprived the Polynesian flora of large-seeded, shade-tolerant species associated with mature continental forests. More generally, island floras harbour a small range of the adaptive solutions to biotic and abiotic stresses relative to more phylogenetically diverse continental floras, and this constraint may increase their susceptibility to invasion. Functional comparisons of native and invasive forest species indicate that such phylogenetic constraints are directly associated with C costs. For example, Pattison et al. (1998) found Hawaiian forest invaders had lower respiratory costs for a given photosynthetic rate than natives, in both sun and partial shade conditions. Funk and Vitousek (2007) found that photosynthetic energy-use efficiency – the ratio of maximum photosynthetic rate to leaf construction cost – was several-fold greater for Hawaiian invaders than natives in closed-canopy forests.

Even within continental regions, adaptations present within native floras depend on the evolutionary history of the region. Some native floras have experienced more extreme climatic histories than others of similar latitude, creating 'empty niches' that have been colonized by functionally distinct invaders (Dansereau, 1964), often facilitated by climate change. For example, Fridley (2013) and

Zohner and Renner (2017) suggested that the environmental history of North American deciduous forests may have predisposed them to invasions from Eurasian woody species, which leaf out earlier and senesce later as a result of more predictable spring and autumnal climate across Eurasia (Fridley, 2012; Zohner & Renner, 2017). Fridley et al. (2022) showed this strategy of extended leaf phenology to be associated with greater shade tolerance through longer leaf life span in invaders despite their greater growth and photosynthetic rates compared with natives; leaf phenology is implicated in other deciduous forest invasions as well, including the spread of *H. dulcis* in subtropical Brazil (Rejmánek, 2013) and *A. platanoides* in temperate North America (Kloeppel & Abrams, 1995). Furthermore, Heberling and Fridley (2013) showed that the ratio of maximum photosynthetic rate to leaf dark respiration rate (A_{sat}/R_d) is significantly greater in North American forest invaders than co-occurring native species and is consistent with a generally greater A_{sat}/R_d ratio for East Asian species compared with North American species (Heberling & Fridley, 2012). For European forests, Closset-Kopp et al. (2007) suggested the invasiveness of the North American native *P. serotina* is due in part to its mid-successional 'sit and wait' strategy of low-light survival and fast gap response that is common in the North American flora but lacking in Europe, potentially as a result of more widespread Pleistocene extinctions in the European tree flora (Eiserhardt et al., 2015).

5 | FROM PERSISTENCE TO DOMINANCE: CARBON BUDGETS AND FOREST LIFE-HISTORY STRATEGIES

Disturbance is critical to forest population dynamics (Woods et al., 2021); even those species typically classified as highly shade-tolerant require short-lived, often repeated pulses of canopy disturbance to reach the canopy and/or support the energy demands of seed production (Canham, 1985; Denslow, 1987). Thus, shade tolerance is not in itself a holistic mechanism of invader dominance in forests; rather, it is a means to persist through a strong selective filter that must be followed by rapid growth and reproduction to achieve dominance (Figure 2). In this way, we suggest that what is most important about the forest superinvader phenotype is the combination of unusually high rates of growth in both high- and low-light conditions, enabling both long persistence in shade and rapid dominance and high seed production when conditions become favourable for reproduction. Such traits include those expressed in both sun and shade; moreover, because both conditions may persist for years or decades, short-term studies may overestimate the importance of any one trait to the invasion process, contributing to reduced generalization of invasion theory through context dependence (Catford et al., 2022). We highlight three general aspects of forest dynamics – establishment and persistence of individuals in shade, the role of canopy disturbances in advanced regeneration and adaptive responses to sudden light availability – in the context of life-history strategies associated with dominance by woody invaders. We

hypothesize that lower C costs of invaders permit an array of strategies in both sun and shade that enable gap preemption, resulting in eventual displacement of native species (Figure 2).

5.1 | Persistence strategies in shade

Although understorey saplings increase light capture by growing towards the canopy (Coble & Cavaleri, 2014), prioritizing apical growth is not the only adaptive strategy for persisting in closed-canopy forests (Figure 2). Traits associated with the 'persistence niche' (Bond & Midgley, 2001), which involve C storage, resprouting and clonal expansion, can all be effective means by which invaders use surplus C to increase light harvesting, survive disturbances (e.g. fire) and enable rapid response to increased light availability. For example, some shade-tolerant invaders such as *B. thunbergii* have multi-stemmed architecture, such that damaged or pathogen-affected stems are replaced by another resprouting at or near the base, resulting in dense, persistent understorey populations (Ehrenfeld, 1999). *P. serotina* saplings form dense stands in the understorey that then self-thin, but many saplings that die above-ground persist by resprouting from their bases, and when canopies open, resprouting frequency increases (Closset-Kopp et al., 2007). Some woody invaders can also enhance their shade persistence through production of adventitious roots from stems contacting the ground (e.g. *M. calvescens*; Meyer, 1996), and when stems of *P. cattleyanum* fall beneath closed canopies, many resprout and are poised to grow rapidly when canopies open (e.g. during tropical cyclones; Shimizu, 2006). Root sprouting is another attribute of some forest invaders. Some exhibit root sprouting only after disturbance (e.g. *P. undulatum*; Campbell & Clarke, 2006), but others do so in undisturbed forests, consolidating and extending invasions (e.g. *E. umbellata*, Franke et al., 2018; *L. lucidum*, Lichstein et al., 2004; *L. sinense*, Hanula & Horn, 2011; *P. cattleyanum*, Huenneke & Vitousek, 1990). Root sprouting results in clonality, close to established individuals in some species (e.g. *B. thunbergii*, Ehrenfeld, 1999) and more distantly in others (e.g. >10 m in *T. sebifera*, Moriya et al., 2017). In the case of invasive *T. sebifera*, clonality allows photosynthates from canopy stems to be directed towards shaded understorey root sprouts which can persist in the shade until the canopy opens (Moriya et al., 2017).

5.2 | Invasion acceleration through canopy disturbances

Foresters have long appreciated that some types of disturbances accelerate rather than 'reset' forest successional dynamics, depending on whether existing understorey individuals survive and respond to increased light conditions (Abrams & Scott, 1989). Forest invasions appear to be a common example of such advanced regeneration because the combination of shade tolerance and rapid growth accentuates the competitive advantage of understorey invaders in disturbed landscapes, particularly where large-scale canopy disturbances increase growth and recruitment rates (Murphy & Metcalfe, 2016). For example, invasion of Tahitian rainforest by *M. calvescens* accelerated dramatically after forest canopy disturbance caused by cyclones. Meyer (1997) suggested that the six cyclones that hit the Society Islands over 2 years acted as a 'revealer' of an already-established shade-tolerant seedling bank. Similar patterns occurred after cyclones damaged forests with *P. undulatum* in Jamaica (Bellingham et al., 2005, 2018), *A. elliptica* in Florida (Horvitz et al., 1998) and *B. javanica* in the Ogasawara Islands (Abe et al., 2020). For those forests less impacted by cyclones, several other widespread canopy disturbances have been found to accelerate invasions through advanced regeneration, including increasing canopy tree mortality from pests and pathogens (Hoven et al., 2017) and fire (Torres et al., 2014). In a meta-analysis, Jauni et al. (2015) showed that an increase in the abundance of invaders following disturbance is more pronounced in forests than other habitats, perhaps because the magnitude of change in light after disturbance is greater in forests than in habitats such as grasslands.

5.3 | Invader dominance through rapid growth and reproduction

If an established shade-tolerant seedling bank of an invader has lower C costs than native species, then surplus C stored in shaded conditions can be rapidly mobilized when light levels increase after disturbance, enabling production of new light-adapted leaves. This is apparent in the rapid physiological acclimation to sudden increases in light levels by invasive shade-tolerant superinvaders (e.g. *B. javanica*, Yamashita et al., 2000; *P. undulatum*, Ball, 2000), which often exceed those of co-occurring native species. Rapid acclimation to increased light has also been shown in seedlings of many other shade-tolerant invaders in Table 1, including *A. platanoides* (Martin & Marks, 2006), *L. lucidum* (Fernandez et al., 2020), *Q. rubra* (Dyderski & Jagodziński, 2019), *P. serotina* (Closset-Kopp et al., 2007), *M. calvescens* (Murphy et al., 2008) and *A. elliptica* (Horvitz et al., 1998). If such plasticity in sapling physiology is coupled with high relative abundance of the invader in an established sapling bank, this can further enhance invasion (Gurevitch et al., 2008). Horvitz et al. (1998) described this as a syndrome of 'seedling-layer oskar winners', in which invaders establish in shade, dominate the sapling bank, then outcompete and suppress native seedlings when light is available through a combination of superior physiological response to light and high abundance.

Rapid acclimation and production of new sun leaves is likely to result in rapid stem elongation and production of more leaves, resulting in significantly increased rates of whole-plant C gain to support reproduction. Some invaders (e.g. *P. serotina*, *Q. rubra*, *R. cathartica*) flower and fruit in the understorey but even these benefit from canopy disturbances through enhanced reproductive effort (Dyderski & Jagodziński, 2018; Knight et al., 2007; Phartyal et al., 2009; Stewart & Graves, 2006). Further, many woody invaders (e.g. *A. platanoides*, *H. dulcis*, *L. lucidum*, *T. sebifera*) are prolific seeders that

can compensate for low population densities with high per capita seed production, which then overrides establishment limitations, increasing their invasive potential. Consequently, even when very few plants are able to initially establish in the understorey, they subsequently overwhelm establishment barriers with copious propagule production (Aguirre-Acosta et al., 2014; Warren et al., 2012). Thus, local dominance and suppression of native species regeneration by forest superinvaders occurs most rapidly when canopy disturbances promote rapid maturity of existing saplings that were able to establish in closed-canopy conditions. We argue that this unusually wide range of survival and growth strategies along a light gradient is the key to understanding forest superinvader dominance and is an expected consequence of reduced C costs.

6 | MANAGEMENT IMPLICATIONS

Invasions of closed-canopy forests by plant species remain limited in many regions; although some of this absence may be due to high biotic resistance of some floras (Fridley & Sax, 2014), slow population dynamics inherent to understorey communities and the relative isolation of many large forest tracts from roads and settlement have slowed the progression of forest invasions compared with other habitats (Martin et al., 2009). One consequence of this forest invasion lag is that managers in many regions have an opportunity to prevent invasions through risk assessment of potential introductions (Křivánek & Pyšek, 2006). Towards this goal, a prediction of our hypothesis is that closed-canopy forests may be prone to invasions by woody species that are uncommon in forested habitat in their native range, because their ability to survive shading should increase as potential C costs decline. Indeed, our conceptual model suggests that, paradoxically, it may be the inherently fast-growing, acquisitive species that have the most to gain from reductions in C costs in the invaded range (Blumenthal, 2006), which not only facilitates their recruitment in shaded sites but also amplifies their advantage under post-disturbance conditions. Although the native range ecology of many of the superinvaders in Table 1 remains understudied, there are several well-known cases where invaders appear more shade-tolerant in their invaded range, and all bear acquisitive functional traits, including *R. cathartica* (Heberling et al., 2016), *M. crenata* (DeWalt et al., 2004), *M. calvescens* (Meyer, 1997) and *S. cooperi* (Medeiros et al., 1992). Thus, managers should bear in mind that habitat-matching criteria in risk assessments may be unreliable predictors of forest invasiveness. On the other hand, we acknowledge that many woody invaders are not generally a threat to forest biodiversity due to limited shade tolerance (e.g. the global invader *Ailanthus altissima*; Martin et al., 2010), for reasons that remain unclear. One hypothesis is that those that remain light-dependent do not experience the same change in C costs in the invaded range as forest superinvaders, but this remains to be tested.

Forest invasions that occur as a result of differences in net C gain between native and invasive species may also alter ecosystem-level C dynamics. All else being equal, a population that experiences lower C costs per unit of assimilation has a higher carbon-use efficiency (CUE), defined as the ratio of net and gross primary production and one of the key determinants of the ability of forests to sequester C (DeLucia et al., 2007). Although some studies of invader impacts on ecosystem C dynamics suggest invaders may increase plant C stocks (Liao et al., 2008), relationships between forest invader traits and long-term ecosystem C dynamics are more complex than implied by the C budgets of individual plants (Peltzer et al., 2010). In particular, the impact of invaders on soil processes, including litter decomposition, is likely to play a larger role in ecosystem-level CUE than direct effects of invader respiration or tissue loss rates. For example, Aerts et al. (2017) showed that the impact of invasive *P. serotina* in European forests on soil respiration rates was driven by its comparatively high litter nutrient content. Nonetheless, as empirical comparisons of individual whole-plant C budgets are rare, it remains difficult to link the C budgets of ecosystems to that of dominant plants, whether native or invasive (Fridley, 2017).

7 | CONCLUSION: SUPERINVADERS AND WHOLE-PLANT C DYNAMICS

Ecological strategies of plant invaders encompass a wide range of functional and life-history traits (Funk, 2013). Although the characterization of invaders as 'ideal weeds' (Baker & Stebbins, 1965) continues to pervade the literature (e.g. Guo et al., 2018), there is a need to distinguish invader phenotypes of strictly ruderal weeds, such as globally ubiquitous annuals like *Chenopodium album*, from those that do not fit neatly within adaptive trade-off frameworks established for native species (Fridley et al., 2022; Moles et al., 2012). We have demonstrated that there is a special class of woody invaders in closed-canopy forests that pose especially grave threats to native biodiversity as a result of 'rule-breaking' behaviour that enables competitive dominance across a wide range of forest conditions. We refer to these species as 'superinvaders' to distinguish them from other invasive species that, although capable of local dominance and fast population spread, have similar ecological strategies to some early successional native species (Davis et al., 2001). The existence of forest superinvaders begs the question as to the physiological basis of such a wide ecological niche, particularly given substantial research into the nature of functional trade-offs along light gradients (Valladares & Niinemets, 2008). We have shown that the forest superinvader phenotype is an expected consequence of reduced C costs in the invaded range; such reduced costs are a potential consequence of enemy release, recent environmental changes that alleviate stress, and phylogenetic constraints in some floras that limit the resource-use efficiency of native species. Other well-known mechanisms, especially local adaptation and phenotypic plasticity, may contribute to the invasiveness of introduced species, but at present there is insufficient evidence to

incorporate them specifically into the C cost framework. If enemy release declines as invaders accumulate pests, or forest environments shift to favour more stress-tolerant phenotypes of some native species, then we predict the dominance of superinvaders will decline. On the other hand, continued resource enrichment, such as N deposition and elevated CO_2, may further accelerate the impacts of woody invaders and elevate other non-native species to 'superinvader' status. Similarly, continued introduction of more resource-efficient species to disharmonic floras such as oceanic islands is likely to further erode native forest diversity.

We are a long way from understanding whole-plant resource dynamics for all but a handful of mostly annual crops and model organisms. As invasion research incorporates advances from functional studies that are increasingly able to monitor plant C allocation to tissues and processes that have been difficult to measure, invasion biologists will be better equipped to test theory based on differences in resource use between native and non-native species. For example, whole-plant C partitioning studies using isotopic pulse-labelling methods are increasingly applied in situ (Epron et al., 2012), allowing important C costs such as rhizodeposition to be included in plant economic strategy theory (Henneron et al., 2020). Our theory of forest invasions based on net C gain suggests a renewed emphasis on such traits that are rarely measured in invasion studies, including rates of tissue loss and respiratory processes above- and below-ground. Such studies would help establish the physiological basis of superinvader behaviour, which can be further quantified by studies of WPLCPs (Lusk & Jorgensen, 2013) across native and invasive species. In turn, a more rigorous mechanistic understanding of forest superinvaders will facilitate more targeted strategies to address what has been thus far one of the more intractable problems in sustainable forest management.

AUTHOR CONTRIBUTIONS

Jason D. Fridley conceptualized the study and led manuscript preparation with input from all authors. All authors edited the manuscript.

CONFLICT OF INTEREST

The authors declare no conflicts of interest. J.D.F. and P.J.B. are editors of *Journal of Ecology* but took no part in the peer review and decision-making processes for this paper.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14001.

DATA AVAILABILITY STATEMENT

This article includes no data.

ORCID

Jason D. Fridley https://orcid.org/0000-0002-0581-376X
Peter J. Bellingham https://orcid.org/0000-0001-9646-4819
Déborah Closset-Kopp https://orcid.org/0000-0001-6319-1332
Michele S. Dechoum https://orcid.org/0000-0002-3484-2498
Patrick H. Martin https://orcid.org/0000-0003-2025-4289
Julissa Rojas-Sandoval https://orcid.org/0000-0001-6620-4741
David Tng https://orcid.org/0000-0001-5135-0922

REFERENCES

Abe, T., Tanaka, N., & Shimizu, Y. (2020). Outstanding performance of an invasive alien tree *Bischofia javanica* relative to native tree species and implications for management of insular primary forests. *PeerJ*, *8*, e9573.

Abrams, M. D., & Scott, M. L. (1989). Disturbance-mediated accelerated succession in two Michigan forest types. *Forest Science*, *35*(1), 42–49.

Aerts, R., Ewald, M., Nicolas, M., Piat, J., Skowronek, S., Lenoir, J., Hattab, T., Garzón-López, C. X., Feilhauer, H., Schmidtlein, S., & Rocchini, D. (2017). Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. *Frontiers in Plant Science*, *8*, 179.

Agrawal, A. A. (2020). A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, *101*(2), e02924.

Aguirre-Acosta, N., Kowaljow, E., & Aguilar, R. (2014). Reproductive performance of the invasive tree *Ligustrum lucidum* in a subtropical dry forest: Does habitat fragmentation boost or limit invasion? *Biological Invasions*, *16*(7), 1397–1410.

Augspurger, C. K., & Kelly, C. K. (1984). Pathogen mortality of tropical tree seedlings: Experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia*, *61*(2), 211–217.

Baker, H. G., & Stebbins, G. L. (1965). *The genetics of colonizing species: Proceedings of the first international union of biological sciences symposia on general biology*. Academic Press.

Ball, T. (2000). *Effect of canopy gaps on tree seedling ecophysiology in a Jamaican montane rainforest* [PhD thesis]. University of Cambridge.

Baltzer, J. L., & Thomas, S. C. (2007a). Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *Journal of Ecology*, *95*(6), 1208–1221.

Baltzer, J. L., & Thomas, S. C. (2007b). Physiological and morphological correlates of whole-plant light compensation point in temperate deciduous tree seedlings. *Oecologia*, *153*(2), 209–223. https://doi.org/10.1007/s00442-007-0722-2

Baruch, Z., Pattison, R. R., & Goldstein, G. (2000). Responses to light and water availability of four invasive Melastomataceae in the Hawaiian islands. *International Journal of Plant Sciences*, *161*(1), 107–118.

Bellingham, P. J., Tanner, E. V. J., & Healey, J. R. (2005). Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. *Journal of Vegetation Science*, *16*(6), 675–684.

Bellingham, P. J., Tanner, E. V. J., 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. https://doi.org/10.1016/j.biocon.2017.10.028

Blumenthal, D. M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, *9*(7), 887–895. https://doi.org/10.1111/j.1461-0248.2006.00934.x

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution*, 16(1), 45–51.

Brown, K. A., Scatena, F. N., & Gurevitch, J. (2006). Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. *Forest Ecology and Management*, 226(1), 145–152. https://doi.org/10.1016/j.foreco.2006.01.031

Butterfield, B. J., Rogers, W. E., & Siemann, E. (2004). Growth of Chinese tallow tree (*Sapium sebiferum*) and four native trees under varying water regimes. *The Texas Journal of Science*, 56(4), 335–347.

Campbell, M. L., & Clarke, P. J. (2006). Response of montane wet sclerophyll forest understorey species to fire: Evidence from high and low intensity fires. *Proceedings of the Linnean Society of New South Wales*, 127, 63–73.

Canham, C. D. (1985). Suppression and release during canopy recruitment in *Acer saccharum*. *Bulletin of the Torrey Botanical Club*, 112(2), 134–145.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., & White, P. S. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research*, 20(5), 620–631.

Carlquist, S. (1974). *Island biology*. Columbia University Press.

Carvalho, P. E. R. (1994). *Ecologia, silvicultura e usos da uva-do-japão (Hovenia dulcis Thunberg)*. Embrapa Florestas-Circular Técnica (INFOTECA-E).

Catford, J. A., Wilson, J. R. U., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, 37(2), 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Chai, S.-L., Healey, J. R., & Tanner, E. V. J. (2012). Evaluation of forest recovery over time and space using permanent plots monitored over 30 years in a Jamaican montane rain forest. *PLoS ONE*, 7(11), e48859. https://doi.org/10.1371/journal.pone.0048859

Cincotta, C. L., Adams, J. M., & Holzapfel, C. (2009). Testing the enemy release hypothesis: A comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). *Biological Invasions*, 11(2), 379–388.

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(1), 120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Coble, A. P., & Cavaleri, M. A. (2014). Light drives vertical gradients of leaf morphology in a sugar maple (*Acer saccharum*) forest. *Tree Physiology*, 34(2), 146–158.

Coomes, D. A., & Grubb, P. J. (2000). Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. *Ecological Monographs*, 70(2), 171–207.

Craine, J., Engelbrecht, B., Lusk, C., McDowell, N., & Poorter, H. (2012). Resource limitation, tolerance, and the future of ecological plant classification. *Frontiers in Plant Science*, 3, 246. https://doi.org/10.3389/fpls.2012.00246

Daehler, C. C. (2003). Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 183–211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403

Dansereau, P. (1964). Six problems in New Zealand vegetation. *Bulletin of the Torrey Botanical Club*, 91(2), 114–140.

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88(3), 528–534.

Davis, M. A., Thompson, K., & Grime, J. P. (2001). Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. *Diversity and Distributions*, 7(1–2), 97–102.

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(6), 823–833. https://doi.org/10.1007/s11258-015-0470-z

DeLucia, E. H., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13(6), 1157–1167.

Denslow, J. S. (1987). Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, 18(1), 431–451.

Denslow, J. S. (2003). Weeds in paradise: Thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden*, 90, 119–127.

DeWalt, S. J. (2006). Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. *Biological Invasions*, 8(5), 1145–1158.

DeWalt, S. J., Denslow, J. S., & Ickes, K. (2004). Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology*, 85(2), 471–483.

Dickie, I. A., Bufford, J. L., Cobb, R. C., Desprez-Loustau, M. L., Grelet, G., Hulme, P. E., Klironomos, J., Makiola, A., Nuñez, M. A., Pringle, A., & Thrall, P. H. (2017). The emerging science of linked plant–fungal invasions. *New Phytologist*, 215(4), 1314–1332.

Diez, J. M., Dickie, I., Edwards, G., Hulme, P. E., Sullivan, J. J., & Duncan, R. P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, 13(7), 803–809.

Drake, D. R., & Mueller-Dombois, D. (1993). Population development of rain forest trees on a chronosequence of Hawaiian lava flows. *Ecology*, 74(4), 1012–1019.

Du, E., & de Vries, W. (2018). Nitrogen-induced new net primary production and carbon sequestration in global forests. *Environmental Pollution*, 242, 1476–1487.

Durand, L. Z., & Goldstein, G. (2001). Photosynthesis, photoinhibition, and nitrogen use efficiency in native and invasive tree ferns in Hawaii. *Oecologia*, 126(3), 345–354.

Dyderski, M. K., & Jagodziński, A. M. (2018). Drivers of invasive tree and shrub natural regeneration in temperate forests. *Biological Invasions*, 20(9), 2363–2379.

Dyderski, M. K., & Jagodziński, A. M. (2019). Seedling survival of *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. in temperate forests of Western Poland. *Forest Ecology and Management*, 450, 117498.

Easdale, T. A., & Healey, J. R. (2009). Resource-use-related traits correlate with population turnover rates, but not stem diameter growth rates, in 29 subtropical montane tree species. *Perspectives in Plant Ecology, Evolution and Systematics*, 11(3), 203–218. https://doi.org/10.1016/j.ppees.2009.03.001

Edgin, B., & Ebinger, J. E. (2001). Control of autumn olive (*Elaeagnus umbellata* Thunb.) at Beall Woods Nature Preserve, Illinois, USA. *Natural Areas Journal*, 21(4), 386–388. https://www.jstor.org/stable/43912026

Ehrenfeld, J. G. (1999). Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii* DC.) in deciduous forests of New Jersey. *Biological Invasions*, 1(2), 203–213.

Eiserhardt, W. L., Borchsenius, F., Plum, C. M., Ordonez, A., & Svenning, J. C. (2015). Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters*, 18(3), 263–272.

Epron, D., Bahn, M., Derrien, D., Lattanzi, F. A., Pumpanen, J., Gessler, A., Högberg, P., Maillard, P., Dannoura, M., Gérant, D., & Buchmann, N. (2012). Pulse-labelling trees to study carbon allocation dynamics: A review of methods, current knowledge and future prospects. *Tree Physiology*, 32(6), 776–798.

Falster, D. S., Duursma, R. A., & FitzJohn, R. G. (2018). How functional traits influence plant growth and shade tolerance across the life cycle. *Proceedings of the National Academy of Sciences of the United States of America*, 115(29), E6789–E6798. https://doi.org/10.1073/pnas.1714044115

Fernandez, R. D., Castro-Díez, P., Aragón, R., & Pérez-Harguindeguy, N. (2021). Changes in community functional structure and ecosystem properties along an invasion gradient by *Ligustrum lucidum. Journal of Vegetation Science*, *32*(6), e13098. https://doi.org/10.1111/jvs.13098

Fernandez, R. D., Ceballos, S. J., Aragón, R., Malizia, A., Montti, L., Whitworth-Hulse, J. I., Castro-Díez, P., & Grau, H. R. (2020). A global review of *Ligustrum lucidum* (Oleaceae) invasion. *The Botanical Review*, *86*(2), 93–118. https://doi.org/10.1007/s12229-020-09228-w

Florens, F. B. V., Baider, C., Martin, G. M. N., Seegoolam, N. B., Zmanay, Z., & Strasberg, D. (2016). Invasive alien plants progress to dominate protected and best-preserved wet forests of an oceanic Island. *Journal for Nature Conservation*, *34*, 93–100. https://doi.org/10.1016/j.jnc.2016.09.006

Fox, M. D., & Fox, B. J. (1986). The susceptibility of natural communities to invasion. In R. H. Groves & J. J. Burdon (Eds.), *Ecology of biological invasions* (pp. 57–66). Cambridge University Press.

Franke, M. E., Zipper, C., & Barney, J. N. (2018). Native hardwood tree seedling establishment following invasive autumn-olive (*Elaeagnus umbellata*) removal on a reclaimed coal mine. *Invasive Plant Science and Management*, *11*(3), 155–161.

Fridley, J. D. (2008). Of Asian forests and European fields: Eastern US plant invasions in a global floristic context. *PLoS ONE*, *3*(11), e3630.

Fridley, J. D. (2012). Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, *485*(7398), 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*(1), 8–17.

Fridley, J. D. (2017). Plant energetics and the synthesis of population and ecosystem ecology. *Journal of Ecology*, *105*(1), 95–110.

Fridley, J. D., Bauerle, T., Craddock, A., Ebert, A., Frank, D., Heberling, J. M., Hinman, E., Jo, I., Martinez, K., Smith, M., Woolhiser, L., & Yin, J. (2022). Fast but steady: An integrated leaf-stem-root trait syndrome for woody forest invaders. *Ecology Letters*, *25*(4), 900–912. https://doi.org/10.1111/ele.13967

Fridley, J. D., & Sax, D. F. (2014). The imbalance of nature: Revisiting a Darwinian framework for invasion biology. *Global Ecology and Biogeography*, *23*(11), 1157–1166.

Funk, J. L. (2013). The physiology of invasive plants in low-resource environments. *Conservation Physiology*, *1*(1), cot026. doi:10.1093/conphys/cot026

Funk, J. L., Parker, I. M., Matzek, V., Flory, S. L., Aschehoug, E. T., D'Antonio, C. M., Dawson, W., Thomson, D. M., & Valliere, J. (2020). Keys to enhancing the value of invasion ecology research for management. *Biological Invasions*, *22*(8), 2431–2445. https://doi.org/10.1007/s10530-020-02267-9

Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, *446*(7139), 1079–1081.

Galetti, M., Bovendorp, R. S., & Guevara, R. (2015). Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. *Global Ecology and Conservation*, *3*, 824–830.

Givnish, T. J. (1988). Adaptation to sun and shade: A whole-plant perspective. *Functional Plant Biology*, *15*(2), 63–92.

Givnish, T. J., Montgomery, R. A., & Goldstein, G. (2004). Adaptive radiation of photosynthetic physiology in the Hawaiian lobeliads: Light regimes, static light responses, and whole-plant compensation points. *American Journal of Botany*, *91*(2), 228–246.

Goodland, T., & Healey, J. R. (1996). *The invasion of Jamaican montane rainforests by the Australian tree Pittosporum undulatum*. School of Agricultural and Forest Sciences, University of Wales Bangor.

Grove, E., & Clarkson, B. D. (2005). *An ecological study of Chinese privet (Ligustrum sinense Lour.) in the Waikato Region* [Working paper]. Centre for Biodiversity and Ecology Research, Department of Biological Sciences, The University of Waikato. https://researchcommons.waikato.ac.nz/handle/10289/3782

Guo, W. Y., van Kleunen, M., Winter, M., Weigelt, P., Stein, A., Pierce, S., Pergl, J., Moser, D., Maurel, N., Lenzner, B., & Kreft, H. (2018). The role of adaptive strategies in plant naturalization. *Ecology Letters*, *1*(9), 1380–1389.

Gurevitch, J., Howard, T. G., Ashton, I. W., Leger, E. A., Howe, K. M., Woo, E., & Lerdau, M. (2008). Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. *Biological Invasions*, *10*(6), 821–831.

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*(1), 257–274.

Hanula, J. L., & Horn, S. (2011). Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. *Forest Ecology and Management*, *262*(4), 674–680.

Hartman, K. M., & McCarthy, B. C. (2008). Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). *Journal of the Torrey Botanical Society*, *135*(2), 245–259.

Hata, K., Suzuki, J. I., Kachi, N., & Yamamura, Y. (2006). A 19-year study of the dynamics of an invasive alien tree, *Bischofia javanica*, on a Subtropical Oceanic Island. *Pacific Science*, *60*(4), 455–470.

Heberling, J. M., & Fridley, J. D. (2012). Biogeographic constraints on the world-wide leaf economics spectrum. *Global Ecology and Biogeography*, *21*(12), 1137–1146.

Heberling, J. M., & Fridley, J. D. (2013). Resource-use strategies of native and invasive plants in Eastern North American forests. *New Phytologist*, *200*(2), 523–533.

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*(4), 874–884.

Heberling, J. M., Jo, I., Kozhevnikov, A., Lee, H., & Fridley, J. D. (2017). Biotic interchange in the Anthropocene: Strong asymmetry in East Asian and Eastern North American plant invasions. *Global Ecology and Biogeography*, *26*(4), 447–458.

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*(6), 875–884.

Henneron, L., Kardol, P., Wardle, D. A., Cros, C., & Fontaine, S. (2020). Rhizosphere control of soil nitrogen cycling: A key component of plant economic strategies. *New Phytologist*, *228*(4), 1269–1282.

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*(5), 633–644.

Horvitz, C. C., Pascarella, J. B., McMann, S., Freedman, A., & Hofstetter, R. H. (1998). Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications*, *8*(4), 947–974. https://doi.org/10.1890/1051-0761(1998)008[0947:FROINI]2.0.CO;2

Hoven, B. M., Gorchov, D. L., Knight, K. S., & Peters, V. E. (2017). The effect of emerald ash borer-caused tree mortality on the invasive shrub Amur honeysuckle and their combined effects on tree and shrub seedlings. *Biological Invasions*, *19*(10), 2813–2836.

Hoyos, L. E., Gavier-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*(9), 3261–3275. https://doi.org/10.1007/s10530-010-9720-0

Huenneke, L. F., & Vitousek, P. M. (1990). Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: Implications for management of native Hawaiian forests. *Biological Conservation*, *53*(3), 199–211.

Jauni, M., Gripenberg, S., & Ramula, S. (2015). Non-native plant species benefit from disturbance: A meta-analysis. *Oikos*, *124*(2), 122–129.

Jolly, W. M., Cochrane, M. A., Freeborn, P. H., Holden, Z. A., Brown, T. J., Williamson, G. J., & Bowman, D. M. J. S. (2015). Climate-induced variations in global wildfire danger from 1979 to 2013. *Nature Communications*, *6*(1), 7537. https://doi.org/10.1038/ncomms8537

Jones, R. H., & McLeod, K. W. (1989). Shade tolerance in seedlings of Chinese tallow tree, American sycamore, and cherrybark oak. *Bulletin of the Torrey Botanical Club*, *116*(4), 371–377.

Jubinsky, G., & Anderson, L. C. (1996). The invasive potential of Chinese tallow-tree (*Sapium sebiferum* Roxb.) in the southeast. *Castanea*, *61*(3), 226–231.

King, D. A. (1994). Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany*, *81*(8), 948–957. https://doi.org/10.1002/j.1537-2197.1994.tb15581.x

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, *98*(3), 419–428. https://doi.org/10.1007/BF00324232

Kloeppel, B. D., & Abrams, M. D. (1995). Ecophysiological attributes of the native *Acer saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, USA. *Tree Physiology*, *15*(11), 739–746.

Knight, K. S., Kurylo, J. S., Endress, A. G., Stewart, J. R., & Reich, P. B. (2007). Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): A review. *Biological Invasions*, *9*(8), 925–937. https://doi.org/10.1007/s10530-007-9091-3

Kobe, R. K. (1997). Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos*, *80*(2), 226–233.

Kobe, R. K., Pacala, S. W., Silander, J. A., Jr., & Canham, C. D. (1995). Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, *5*(2), 517–532.

Kong, D., & Fridley, J. D. (2019). Does plant biomass partitioning reflect energetic investments in carbon and nutrient foraging? *Functional Ecology*, *33*(9), 1627–1637.

Krishnadas, M., & Comita, L. S. (2018). Influence of soil pathogens on early regeneration success of tropical trees varies between forest edge and interior. *Oecologia*, *186*(1), 259–268.

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 and Distributions*, *12*(3), 319–327.

Kuehne, C., Nosko, P., Horwath, T., & Bauhus, J. (2014). A comparative study of physiological and morphological seedling traits associated with shade tolerance in introduced red oak (*Quercus rubra*) and native hardwood tree species in southwestern Germany. *Tree Physiology*, *34*(2), 184–193. https://doi.org/10.1093/treephys/tpt124

Kurylo, J. S., Knight, K. S., Stewart, J. R., & Endress, A. G. (2007). *Rhamnus cathartica*: Native and naturalized distribution and habitat preferences. *Journal of the Torrey Botanical Society*, *134*(3), 420–430.

Landrum, L. R. (2017). *The genus Psidium (Myrtaceae) in the state of Bahia, Brazil*. Herbarium, Natural History Collections, School of Life Sciences.

Larrue, S., Daehler, C. C., Meyer, J. Y., Pouteau, R., & Voldoire, O. (2015, September 20). Distribution, abundance and photosynthetic characteristics of the invasive tree Spathodea campanulata on the Island of Tahiti (South Pacific Ocean). In *EMAPi 2015: 13th international conference of ecology and Management of Alien Plant Invasions*. HAL-Inria (online). https://hal.archives-ouvertes.fr/hal-01226561

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, *7*(10), 975–989.

Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., & Li, B. (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: A meta-analysis. *New Phytologist*, *177*(3), 706–714. https://doi.org/10.1111/j.1469-8137.2007.02290.x

Lichstein, J. W., Grau, H. R., & Aragón, R. (2004). Recruitment limitation in secondary forests dominated by an exotic tree. *Journal of Vegetation Science*, *15*(6), 721–728.

Lieurance, D., & Landsbergen, K. (2016). The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae). *Journal of the Torrey Botanical Society*, *143*(4), 415–426.

Linderholm, H. W. (2006). Growing season changes in the last century. *Agricultural and Forest Meteorology*, *137*(1–2), 1–14.

Link, A. F., Turnblacer, T., Snyder, C. K., Daugherty, S. E., & Utz, R. M. (2018). Low recruitment of native trees in a deciduous forest associated with Japanese barberry (*Berberis thunbergii*) invasion. *Invasive Plant Science and Management*, *11*(1), 20–26.

Liu, Y., Oduor, A. M., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M. R., Xu, X., & Van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, *23*(8), 3363–3370.

Loewenstein, N. J., & Loewenstein, E. F. (2005). Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. *Urban Ecosystem*, *8*(1), 79–91. https://doi.org/10.1007/s11252-005-1420-7

Lugo, A. E. (2004). The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment*, *2*(5), 265–273.

Luken, J. O., & Goessling, N. (1995). Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *American Midland Naturalist*, *133*(1), 124–130.

Luken, J. O., Kuddes, L. M., Tholemeier, T. C., & Haller, D. M. (1997). Comparative responses of *Lonicera maackii* (Amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. *American Midland Naturalist*, *138*(2), 331–343.

Luken, J. O., & Thieret, J. W. (1996). Amur honeysuckle, its fall from grace. *Bioscience*, *46*(1), 18–24.

Lusk, C. H., & Jorgensen, M. A. (2013). The whole-plant compensation point as a measure of juvenile tree light requirements. *Functional Ecology*, *27*(6), 1286–1294. https://doi.org/10.1111/1365-2435.12129

Lusk, C. H., Jorgensen, M. A., & Bellingham, P. J. (2015). A conifer–angiosperm divergence in the growth vs. shade tolerance trade-off underlies the dynamics of a New Zealand warm-temperate rain forest. *Journal of Ecology*, *103*(2), 479–488. https://doi.org/10.1111/1365-2745.12368

Major, K. C., Nosko, P., Kuehne, C., Campbell, D., & Bauhus, 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. https://doi.org/10.1016/j.foreco.2012.12.006

Marciniak, B., Dechoum, M., & Castellani, T. T. (2020). The danger of non-native gardens: Risk of invasion by *Schefflera arboricola* associated with seed dispersal by birds. *Biological Invasions*, *22*(3), 997–1010.

Martin, P. H. (1999). Norway maple (*Acer platanoides*) invasion of a natural forest stand: Understory consequence and regeneration pattern. *Biological Invasions*, *1*(2), 215–222.

Martin, P. H., & Canham, C. D. (2010). Dispersal and recruitment limitation in native versus exotic tree species: Life-history strategies and Janzen-Connell effects. *Oikos*, *119*(5), 807–824.

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*(4), 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*(3), 142–149.

Martin, P. H., & Marks, P. L. (2006). Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). *Journal of Ecology*, *94*(6), 1070–1079.

Martin, P. H., Sherman, R. E., & Fahey, T. J. (2004). Forty years of tropical forest recovery from agriculture: Structure and floristics of secondary and old-growth riparian forests in The Dominican Republic. *Biotropica*, *36*(3), 297–317.

McCarthy-Neumann, S., & Kobe, R. K. (2008). Tolerance of soil pathogens co-varies with shade tolerance across species of tropical tree seedlings. *Ecology*, *89*(7), 1883–1892.

Medeiros, A. C., Loope, L. L., Flynn, T., Anderson, S. J., Cuddihy, L. W., & Wilson, K. A. (1992). Notes on the status of an invasive Australian tree fern (*Cyathea cooperi*) in Hawaiian rain forests. *American Fern Journal*, *82*(1), 27–33.

Medvecká, J., Jarolímek, I., Hegedüšová, K., Škodová, I., Bazalová, D., Botková, K., & Šibíková, M. (2018). Forest habitat invasions – Who with whom, where and why. *Forest Ecology and Management*, *409*, 468–478. https://doi.org/10.1016/j.foreco.2017.08.038

Menzel, A., Hempel, S., Klotz, S., Moora, M., Pyšek, P., Rillig, M. C., Zobel, M., & Kühn, I. (2017). Mycorrhizal status helps explain invasion success of alien plant species. *Ecology*, *98*(1), 92–102.

Meyer, J.-Y. (1996). Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). *Pacific Science*, *50*(1), 66–76.

Meyer, J.-Y. (1997). Epidemiology of the invasion by *Miconia calvescens* and reasons for a spectacular success. In J. Y. Meyer & C. W. Smith (Eds.), *Proceedings of the first regional conference on miconia control* (pp. 4–26). University of Hawaii/Centre ORSTOM de Tahiti.

Meyer, J.-Y. (2004). Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. *Pacific Science*, *58*(3), 357–375.

Meyer, J.-Y., & Florence, J. (1996). Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). *Journal of Biogeography*, *23*(6), 775–781.

Moles, A. T., Flores-Moreno, H., Bonser, S. P., Warton, D. I., Helm, A., Warman, L., Eldridge, D. J., Jurado, E., Hemmings, F. A., Reich, P. B., & Cavender-Bares, J. (2012). Invasions: The trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology*, *100*(1), 116–127.

Montesinos, D. (2022). Fast invasives fastly become faster: Invasive plants align largely with the fast side of the plant economics spectrum. *Journal of Ecology*, *110*(5), 1010–1014.

Moriya, Y. D., Nanami, S., Sumikura, J., Yamakura, T., & Itoh, A. (2017). Clonal structure, growth pattern and preemptive space occupancy through sprouting of an invasive tree, *Triadica sebifera*. *Journal of Forest Research*, *22*(1), 8–14. https://doi.org/10.1080/13416979.2016.1265757

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*(6), 1001–1010. https://doi.org/10.1086/342632

Murphy, H. T., Hardesty, B. D., Fletcher, C. S., Metcalfe, D. J., Westcott, D. A., & Brooks, S. J. (2008). Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests. *Biological Invasions*, *10*(6), 925–936.

Murphy, H. T., & Metcalfe, D. J. (2016). The perfect storm: Weed invasion and intense storms in tropical forests. *Austral Ecology*, *41*(8), 864–874.

Mutz, J., McClory, R., van Dijk, L. J., Ehrlén, J., & Tack, A. J. (2021). Pathogen infection influences the relationship between spring and autumn phenology at the seedling and leaf level. *Oecologia*, *197*(2), 447–457.

Naumann, J. C., Bissett, S. N., Young, D. R., Edwards, J., & Anderson, J. E. (2010). Diurnal patterns of photosynthesis, chlorophyll fluorescence, and PRI to evaluate water stress in the invasive species, *Elaeagnus umbellata* Thunb. *Trees*, *24*(2), 237–245. https://doi.org/10.1007/s00468-009-0394-0

Nestby, R. D. (2020). The status of *Prunus padus* L. (bird cherry) in forest communities throughout Europe and Asia. *Forests*, *11*(5), 497.

Niinemets, Ü. (1998). Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap-understory continuum: Interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. *International Journal of Plant Sciences*, *159*(2), 318–330.

Niinemets, Ü. (2006). The controversy over traits conferring shade-tolerance in trees: Ontogenetic changes revisited. *Journal of Ecology*, *94*(2), 464–470. https://doi.org/10.1111/j.1365-2745.2006.01093.x

Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and 'mesophication' of forests in the eastern United States. *Bioscience*, *58*(2), 123–138.

Ostertag, R., Cordell, S., Michaud, J., Cole, T. C., Schulten, J. R., Publico, K. M., & Enoka, J. H. (2009). Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. *Ecosystems*, *12*(3), 503–515. https://doi.org/10.1007/s10021-009-9239-3

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Jr., Kobe, R. K., & Ribbens, E. (1996). Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs*, *66*(1), 1–43.

Pascarella, J. B., Aide, T. M., Serrano, M. I., & Zimmerman, J. K. (2000). Land-use history and forest regeneration in the Cayey mountains, Puerto Rico. *Ecosystems*, *3*(3), 217–228. https://doi.org/10.1007/s100210000021

Pascarella, J. B., & Horvitz, C. C. (1999). Seed and seedling ecology of the invasive non-indigenous shrub *Ardisia elliptica* Thunb. (Myrsinaceae) in South Florida. In *Proceedings of the Twenty Fifth Annual Conference on Ecosystems Restoration and Creation*. Hillsborough Community College.

Pattison, R. R., Goldstein, G., & Ares, A. (1998). Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia*, *117*(4), 449–459.

Peltzer, D. A., Allen, R. B., Lovett, G. M., Whitehead, D., & Wardle, D. A. (2010). Effects of biological invasions on forest carbon sequestration. *Global Change Biology*, *16*(2), 732–746. https://doi.org/10.1111/j.1365-2486.2009.02038.x

Perkins, S. E., Altizer, S., Bjornstad, O., Burdon, J. J., Clay, K., Gómez-Aparicio, L., Jeschke, J. M., Johnson, P. T., Lafferty, K. D., Malmstrom, C. M., Martin, P. H., Power, A., Thrall, P., Strayer, D., & Uriarte, M. (2008). Invasion biology and parasitic infections. In R. S. Ostfeld, F. Keesing, & V. T. Eviner (Eds.), *Ecology of infectious disease: Effects of ecosystems on disease and of disease on ecosystems* (pp. 179–204). Princeton University Press.

Petrovska, R., Brang, P., Gessler, A., Bugmann, H., & Hobi, M. L. (2021). Grow slowly, persist, dominate—Explaining beech dominance in a primeval forest. *Ecology and Evolution*, *11*(15), 10077–10089.

Phartyal, S. S., Godefroid, S., & Koedam, N. (2009). Seed development and germination ecophysiology of the invasive tree *Prunus serotina* (Rosaceae) in a temperate forest in Western Europe. *Plant Ecology*, *204*(2), 285–294.

Pintó-Marijuan, M., & Munné-Bosch, S. (2013). Ecophysiology of invasive plants: Osmotic adjustment and antioxidants. *Trends in Plant Science*, *18*(12), 660–666.

Poorter, L., Wright, S. J., Paz, H., Ackerly, D. D., Condit, R., Ibarra-Manríquez, G., Harms, K. E., Licona, J. C., Martinez-Ramos, M., Mazer, S. J., & Muller-Landau, H. C. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, *89*(7), 1908–1920.

Qaderi, M. M., Clements, D. R., & Cavers, P. B. (2009). The biology of Canadian weeds. 139. *Rhamnus cathartica* L. *Canadian Journal of Plant Science*, *89*(1), 169–189. https://doi.org/10.4141/CJPS08022

Ramsfield, T. D., Bentz, B. J., Faccoli, M., Jactel, H., & Brockerhoff, E. G. (2016). Forest health in a changing world: Effects of globalization and climate change on forest insect and pathogen impacts. *Forestry*, *89*(3), 245–252.

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*(2), 275–301.

Rejmánek, M. (1996). A theory of seed plant invasiveness: The first sketch. *Biological Conservation*, *78*(1–2), 171–181.

Rejmánek, M. (2013). Extended leaf phenology: A secret of successful invaders? *Journal of Vegetation Science*, *24*(6), 975–976.

Rejmánek, M. (2014). Invasive trees and shrubs: Where do they come from and what we should expect in the future? *Biological Invasions*, *16*(3), 483–498. https://doi.org/10.1007/s10530-013-0603-z

Rejmanek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, *77*(6), 1655–1661.

Schultheis, E. H., Berardi, A. E., & Lau, J. A. (2015). No release for the wicked: Enemy release is dynamic and not associated with invasiveness. *Ecology*, *96*(9), 2446–2457.

Schumacher, E., Kueffer, C., Tobler, M., Gmür, V., Edwards, P. J., & Dietz, H. (2008). Influence of drought and shade on seedling growth of native and invasive trees in the Seychelles. *Biotropica*, *40*(5), 543–549.

Schuster, M. J., Wragg, P. D., Williams, L. J., Butler, E. E., Stefanski, A., & Reich, P. B. (2020). Phenology matters: Extended spring and autumn canopy cover increases biotic resistance of forests to invasion by common buckthorn (*Rhamnus cathartica*). *Forest Ecology and Management*, *464*, 118067. https://doi.org/10.1016/j.foreco.2020.118067

Sendall, K. M., Lusk, C. H., & Reich, P. B. (2016). Trade-offs in juvenile growth potential vs. shade tolerance among subtropical rain forest trees on soils of contrasting fertility. *Functional Ecology*, *30*(6), 845–855. https://doi.org/10.1111/1365-2435.12573

Shimizu, Y. (2006). Population dynamics of an invasive plant (*Psidium cattleianum*) after two continuous disturbances in the *Pinus–Schima* secondary forest on Chichijima in the Ogasawara (Bonin) islands. *Regional Views*, *19*, 1–15.

Shouman, S., Mason, N., Heberling, J. M., Kichey, T., Closset-Kopp, D., Kobeissi, A., & Decocq, G. (2020). Leaf functional traits at home and abroad: A community perspective of sycamore maple invasion. *Forest Ecology and Management*, *464*, 118061.

Silander, J. A., & Klepeis, D. M. (1999). The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biological Invasions*, *1*(2), 189–201. https://doi.org/10.1023/A:1010024202294

Soley, N. M., & Sipes, S. D. (2021). Reproductive biology and pollinators of the invasive shrub Autumn olive (*Elaeagnus umbellata* Thunberg). *Plant Species Biology*, *36*(2), 170–186. https://doi.org/10.1111/1442-1984.12307

Stewart, J. R., & Graves, W. R. (2006). Photosynthesis, growth, carbon allocation, and fruit load of *Frangula caroliniana* and *Rhamnus cathartica*. *International Journal of Plant Sciences*, *167*(6), 1161–1168. https://doi.org/10.1086/507650

Stromayer, K. A., & Warren, R. J. (1997). Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin*, *25*(2), 227–234.

Thompson, J., Lugo, A. E., & Thomlinson, J. (2007). Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. *Plant Ecology*, *192*(2), 289–301. https://doi.org/10.1007/s11258-007-9318-5

Tng, D. Y. P., Goosem, M. W., Paz, C. P., Preece, N. D., Goosem, S., Fensham, R. J., & Laurance, S. G. W. (2016). Characteristics of the *Psidium cattleianum* invasion of secondary rainforests. *Austral Ecology*, *41*(4), 344–354. https://doi.org/10.1111/aec.12319

Torres, R. C., Giorgis, M. A., Trillo, C., Volkmann, L., Demaio, P., Heredia, J., & Renison, D. (2014). Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina. *Austral Ecology*, *39*(3), 346–354.

Valladares, F., Allen, M. T., & Pearcy, R. W. (1997). Photosynthetic responses to dynamic light under field conditions in six tropical rainforest shrubs occuring along a light gradient. *Oecologia*, *111*(4), 505–514.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, *39*(1), 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*(2), 235–245.

Vanhellemont, M., Baeten, L., Verbeeck, H., Hermy, M., & Verheyen, K. (2011). Long-term scenarios of the invasive black cherry in pine-oak forest: Impact of regeneration success. *Acta Oecologica*, *37*(3), 203–211. https://doi.org/10.1016/j.actao.2011.02.003

Von Holle, B., Delcourt, H. R., & Simberloff, D. (2003). The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science*, *14*(3), 425–432.

Waddell, E. H., Chapman, D. S., Hill, J. K., Hughes, M., Sailim, A. B., Tangah, J., & Banin, L. F. (2020). Trait filtering during exotic plant invasion of tropical rainforest remnants along a disturbance gradient. *Functional Ecology*, *34*(12), 2584–2597. https://doi.org/10.1111/1365-2435.13679

Walters, M. B., & Reich, P. B. (2000). Trade-offs in low-light CO_2 exchange: A component of variation in shade tolerance among cold temperate tree seedlings. *Functional Ecology*, *14*(2), 155–165. https://doi.org/10.1046/j.1365-2435.2000.00415.x

Warren, R. J., Bahn, V., & Bradford, M. A. (2012). The interaction between propagule pressure, habitat suitability and density-dependent reproduction in species invasion. *Oikos*, *121*(6), 874–881.

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*(7), 366–374.

Woods, K. D., Nagel, T. A., Brzeziecki, B., Cowell, C. M., Firm, D., Jaloviar, P., Kucbel, S., Lin, Y., Maciejewski, Z., Szwagrzyk, J., & Vencurik, J. (2021). Multi-decade tree mortality in temperate old-growth forests of Europe and North America: Non-equilibrial dynamics and species-individualistic response to disturbance. *Global Ecology and Biogeography*, *30*(6), 1311–1333. https://doi.org/10.1111/geb.13291

Woziwoda, B., Potocki, M., Sagan, J., Zasada, M., Tomusiak, R., & Wilczyński, S. (2014). Commercial forestry as a vector of alien tree species—The case of *Quercus rubra* L. introduction in Poland. *Baltic Forestry*, *20*, 131–141.

Wyckoff, P. H., & Webb, S. L. (1996). Understory influence of the invasive Norway maple (*Acer platanoides*). *Bulletin of the Torrey Botanical Club*, *123*(3), 197–205. https://doi.org/10.2307/2996795

Yamashita, N., Ishida, A., Kushima, H., & Tanaka, N. (2000). Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. *Oecologia*, *125*(3), 412–419.

Yamashita, N., Koike, N., & Ishida, A. (2002). Leaf ontogenetic dependence of light acclimation in invasive and native subtropical trees of different successional status. *Plant, Cell & Environment*, *25*(10), 1341–1356.

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*(1), 15–24.

Yazaki, K., Sano, Y., Fujikawa, S., Nakano, T., & Ishida, A. (2010). Response to dehydration and irrigation in invasive and native saplings: Osmotic adjustment versus leaf shedding. *Tree Physiology*, *30*(5), 597–607.

Zhang, Z., Liu, Y., Yuan, L., Weber, E., & van Kleunen, M. (2021). Effect of allelopathy on plant performance: A meta-analysis. *Ecology Letters*, *24*(2), 348–362.

Zhao, J., & Chen, J. (2011). Photosynthesis, growth and foliar herbivory of four *Ardisia* species (Myrsinaceae). *Acta Oecologica*, *37*(3), 277–283. https://doi.org/10.1016/j.actao.2011.02.012

Zohner, C. M., Mo, L., Renner, S. S., Svenning, J. C., Vitasse, Y., Benito, B. M., Ordonez, A., Baumgarten, F., Bastin, J. F., Sebald, V., & Reich, P. B. (2020). Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(22), 12192–12200.

Zohner, C. M., & Renner, S. S. (2017). Innately shorter vegetation periods in North American species explain native–non-native phenological asymmetries. *Nature Ecology & Evolution*, *1*(11), 1655–1660.