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Plant invasions across the Northern Hemisphere: a deep-time perspective

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Few invasion biologists consider the long-term evolutionary context of an invading organism and its invaded ecosystem. Here, I consider patterns of plant invasions across Eastern North America, Europe, and East/Far East Asia, and explore whether biases in exchanges of plants from each region reflect major selection pressures present within each region since the late Miocene, during which temperate Northern Hemisphere floras diverged taxonomically and ecologically. Although there are many exceptions, the European flora appears enriched in species well adapted to frequent, intense disturbances such as cultivation and grazing; the North American composite (Asteraceae) flora appears particularly well adapted to nutrient-rich meadows and forest openings; and the East Asian flora is enriched in shade-tolerant trees, shrubs, and vines of high forest-invasive potential. I argue that such directionality in invasions across different habitat types supports the notion that some species are preadapted to become invasive as a result of differences in historical selection pressures between regions.

Keywords: preadaptation; Eastern North America; naturalized plants; invasion biology

Introduction

Modern biologists are accustomed to treating the introduction and escape of an organism into a new ecosystem as an invasion, particularly in the wake of Charles Elton's classic work that helped define the vibrant subdiscipline of invasion biology.[1,2] As Elton was well aware, however, paleontologists have long considered the process of a species inhabiting a novel environment as a natural component of biotic exchange between regions of disparate evolutionary histories, with species migrating to new ecosystems as the result of repeated shifts of land masses and sea levels over the past 400 million years.[3,4] Although most invasions today are the result of human introduction rather than natural migration, they nonetheless occur within a global evolutionary context that has often produced organisms of strikingly different form and function for a given environmental setting.[5] Thus, modern invasions can be seen as only the latest example of a long history of biotic interchanges between global faunal and floristic regions.[6]

Against this backdrop, it is surprising that so few invasion biologists consider the deep time evolutionary histories of an introduced species and its incipient ecosystem, despite explicit calls for a research agenda that views invasions from the perspective of biotic exchanges between regions.[6,7] For example, studies designed to understand how a species becomes invasive in a given habitat typically focus on traits of the invader in relation to properties of the invaded community (e.g., Is there an empty niche or unconsumed resource? Is the invader lacking enemies that limit native populations?), without considering properties of the invader's native region that might preadapt it for success in a foreign environment. In the absence of a larger context that considers properties of both the invaded region and the source region of invaders, researchers may be ill-equipped to answer some of the most compelling questions of invasion biology: Why are some regions (e.g., tropics) so rarely invaded? Why are species native to certain regions (e.g., Europe) so well represented as global invaders? Why are certain lineages (e.g., *Pinus* in the Southern Hemisphere)

particularly invasive? Why are certain species (e.g., *Acacia mearnsii*, *Lantana camara*, *Spartina anglica*) invasive no matter where they have been introduced?

Here, I explore the modern exchange of plants across the Northern Hemisphere (NH), focusing on linkages of other NH vascular floras to that of Eastern North America (ENA). My first objective is to identify, for certain broadly defined habitats, whether plant invasions across the NH are directional—that is, accounting for differences in introduction effort, are introduced species from one region more likely to become invasive in a given habitat type? A second objective is to ask whether such biases, when found, are consistent with differences in the evolutionary (deep time) histories of the invading organism and its invaded region. For the first objective, I build on previous analysis[8] that identified biases in invader provenance across different habitat types of the Eastern United States (EUS), updated here to include provenance data at the country or subcountry scale for over 2000 EUS-naturalized and invasive species, plus several recently published accounts (see below) of the naturalized and invasive floras of regions across Europe, East Asia, and the Russian Far East. Because information on invaders to ENA from Western North America is less reliable than intercontinental invasions and they are likely a relatively small component of the invasive flora, I restrict my analysis to ENA and Eurasia. For the secondary objective, I consider in broad terms the paleo-floristic records of ENA, Europe, and East Asia and particularly the history of closed (forested) versus open habitats (meadows, fields, woodlands, savannas) over the last 10–12 million years, the period during which strong floristic provincialism developed across the NH. In tying together modern invasion patterns and the evolutionary history of these floras, I then make the case that some species appear to be preadapted as invaders: that is, they have evolved superior adaptations to particular selection pressures (e.g., grazing) that ultimately drive their success in a new region.

I begin by briefly describing the history of modern plant introductions to ENA, to set the stage for an analysis of the invasiveness of species from particular floristic regions that accounts for biases in the number of plant introductions among regions.

Introduction of foreign plants to Eastern North America

Post-Columbian plant introductions into Eastern North America came in two waves, the first consisting of species almost entirely from Europe (between around 1500 and 1850 A.D.) and the second dominated by introductions from East Asia starting in the late 1800s.[9–11] Those of the first wave were concomitant with European settlement, including crops, forage species, and weeds associated with forest clearing, annual cultivation, grazing, and human habitation.[10] The earliest account of naturalized plants in New England, by the Englishman John Josselyn in 1671, emphasized their association with livestock,[9] and there would have been few native species in ENA suitable for productive forage, in part because most native grasses and small forbs are not evergreen or active in early spring or late autumn.[12] Woody species were a small minority of the introductions, and appeared first as fruit trees and a few ornamentals (e.g., *Buxus sempervirens*), followed by a more avid horticultural exchange between American and European gardens from 1750 to 1850.[13]

A second wave of introductions began in 1861 with the first direct shipment of Japanese plants to Eastern U.S. gardens.[13] In contrast to plants introduced in the centuries before, those of the late 19th and early 20th centuries were typically woody and sourced directly from collecting trips in China, Korea, and Japan.[13] Unlike the majority of the European introductions, many East Asian species became garden escapes within a few decades of their introduction.[9] Merhoff[9] and Boufford[10] describe two presentations given by the Harvard botanist M. L. Fernald on nonnative species in New England, one in 1905 and the other in 1940. The first focused almost exclusively on European species with little concern over invaders, while the second focused on escaped garden plants and growing concerns about the effects of invaders on natural areas. Today, the ENA naturalized flora can be largely described as two distinct floras: one European, present in ENA for several centuries and nearly exclusive to the transformed landscapes of human settlement; and another East Asian, relatively recent, and more likely to invade the region's forested natural areas.[8,10]
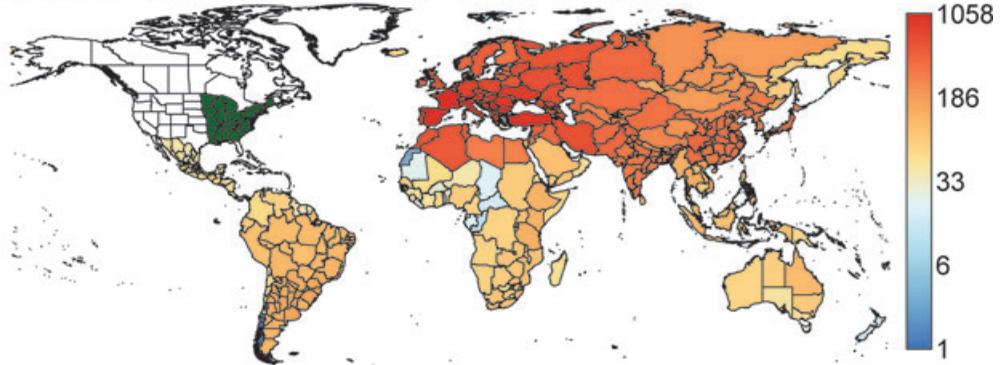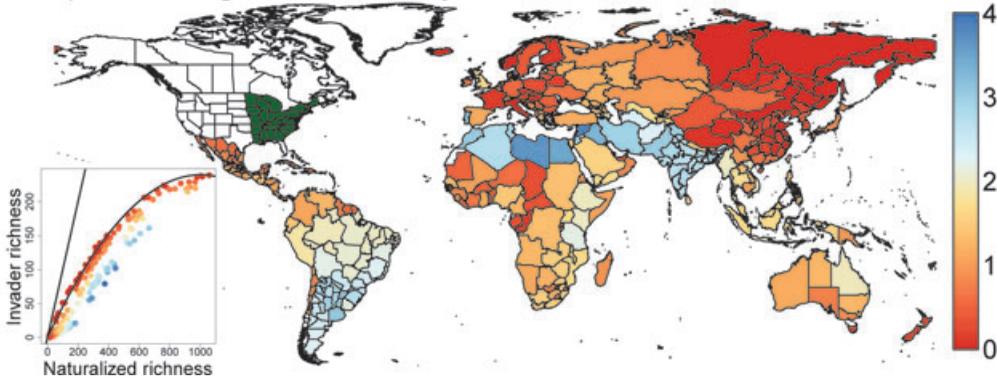
Figure 1. Top: the number of naturalized plants in the Eastern United States (green region) by country or region of origin, according to Ref. 15. Bottom: the number of invasive plants in the Eastern United States by country or region of origin, expressed as a function of the total number of naturalized plants from the same region (graph insert, lower left). A maximum constraint line (95th quantile) describing the relationship between country naturalized and invasive richness was determined as Invader richness = $0.447 \times$ (Nat'zd richness) $- 0.00237 \times$ (Natz'd richness)^2 (curved line, insert; straight line is 1:1 relationship). Residuals from this line are expressed as standard deviations. Regions in red have the maximum number of invaders from their naturalized pool, while species of those regions in blue are less invasive than expected.

Global hotspots of where ENA invaders come from

Five hundred years of plant introductions, habitat modification, and landscape disturbance have led to a vast reorganization of plant communities across ENA. Although the major waves of introduction have come broadly from Europe and East Asia, it is an open question as to how the overall ENA flora is changing in the context of the global distribution of plants and ecosystems. Do the new dominant species come from particular regions, thus increasing the ecological similarity of ENA to specific foreign ecosystems?

To illustrate which regions of the globe are home to species that become particularly invasive after in-

troduction into ENA, I present a geographic analysis of the compiled home ranges of all vascular plant species known to be naturalized in the Eastern U.S. region of ENA, as reported by USDA PLANTS,[14] using a database of native range occurrences compiled by the Germplasm Resources Information Network.[15] The naturalized flora is that reported by Fridley,[8] covering the extent of the eastern deciduous forest of North America[16] and the North American Atlantic floristic region,[17] including the states from Minnesota to Louisiana and eastward, excluding Florida (green region, Fig. 1). For each of the 2682 naturalized species reported by Fridley.[8] I assigned a list of home range occurrences, following the global geographic units of Hollis and Brummitt,[18] as depicted in Figure 1 (mostly at the

country level, with larger countries divided into major provinces). I did not consider taxa at the subspecific or varietal level, and eliminated those species of unknown provenance or those of cultivation origin, resulting in a final dataset of the native geographic occurrences of 2238 naturalized species.

The top panel of Figure 1 shows the total number of EUS-naturalized plants by geographic region of origin, from a maximum of 1058 species native to Italy to zero species native to most oceanic islands. The current EUS-naturalized flora is dominated by European natives, particularly those from the northern section of the Mediterranean Basin from Spain to Turkey (Fig. 1). Few EUS-naturalized species come from the tropics or the Southern Hemisphere. Indeed, native provenances of the EUS-naturalized flora roughly follow from the history of plant introductions, being essentially Eurasian and predominantly European.[19]

A different story emerges, however, if the EUS-naturalized pool is restricted to those that have been reported as invasive by EUS management agencies, a subset of 449 species summarized by Fridley.[8] With all else being equal, regions that have contributed more naturalized species should also contribute more invaders, so a more interesting statistic than the number of EUS invaders native to each region is how much a region deviates from its expected number of invaders, given the size of its naturalized pool. It is not clear a priori what this relationship should be; a graph of the relationship (inset, Fig. 1) suggests the number of invaders from a region levels off after a linear increase with number of naturalized species. I fit a constraint line to these data as a quadratic 95th-quantile regression, and calculated residuals from this line as standard deviations. Regions in red show the empirical maximum number of invaders based on their overall naturalized pool, while species of those regions in blue are less invasive than expected. When shown this way, Europe and East/Far East Asia strongly stand out as regions whose naturalized plants are highly invasive in ENA, and plants of several other regions show a very low invasive tendency, including central Asia, the Indian subcontinent, and many Mediterranean countries. This approach to measuring region invasiveness has shortcomings, however, particularly for those countries that are the source of few naturalized species (central Africa, New Zealand) that appear as invader source hotspots

simply because invader richness is constrained by zero.

Interestingly, historical differences in the type of species introduced from Europe and East Asia—largely herbaceous in the former and woody in the latter—are also reflected in the invasiveness of species from these regions. This was addressed by Fridley,[8] who showed strong biases in the East Asian invader pool toward those invasive in forests and of woody growth form (39% of all East Asian invaders, compared to 23% and 24% of the EUS-native and EUS-naturalized floras, respectively). In the present analysis, woody species account for only 9% of the EUS invaders from many European countries, including Italy, France, Germany, Denmark, and the Ukraine. Further, the predominance of woody growth forms in the invasive species pools of East Asian regions extends to trees, shrubs, and vines: the highest percentages by region for trees are the Russian Far East (20–30%, e.g., Kuril Islands, Amur, Primorye) and Southeast Asia (Laos, Vietnam, Taiwan, Cambodia); those for shrubs include China (especially north central), Japan, and Korea (around 25%); and those for vines include Japan (12%) in addition to regions of far fewer naturalized species (e.g., South American subtropics). Further, of the 74 species invasive in the EUS that are endemic to East Asia, 64 are woody. In contrast, European invaders are closely associated with more open, regularly disturbed ecosystems and are overwhelmingly herbaceous (e.g., 79% of those from Italy).

ENA natives invading other regions: the case of meadow asters

Few habitats in ENA appear resistant to plant invasions, and broad classes of habitats—forests versus disturbed areas, for example—appear to be invaded by species from different geographic and evolutionary contexts. Is this true of the nonnative floras of other regions in the Northern Hemisphere? If many ENA plants have difficulty competing with European or East Asian species in their native habitats, are ENA species therefore less likely to be invasive in Europe or East Asia?

Across East Asia and the Russian Far East, where most nonnative floras have only recently been catalogued, ENA natives do appear to have made significant contributions to the nonnative pool, but only in particular habitats and with a strong taxonomic bias. For example, Weber et al.[20] list 33 species of

invasive plants in China endemic to North America, nearly half (16) of which are composites (Asteraceae), substantially greater than the overall percentage of Asteraceae in the Chinese invasive flora (19%, or 52 species out of 270). This percentage is nearly equal to that of North American species in the Korean naturalized flora,[21] 32 (of 76) of which are in the Asteraceae, whereas in the whole naturalized flora Asteraceae accounts for 68 species out of 321 (21%). For the Russian Far East, Asteraceae composes the largest group of aliens (123 species, 18%), many of which are also from ENA.[22] Overall, Asteraceae species that are naturalized or invasive across much of East/Far East Asia appear to be common ENA meadow species, including species of *Solidago, Erigeron, Helianthus, Symphyotrichum* (formerly *Aster*)*, Bidens, Coreopsis, Ambrosia, Conyza, Xanthium, Rudbeckia,* and *Ageratina* (formerly *Eupatorium*).

In contrast, woody species are poorly represented in East Asian nonnative floras, and the few that are represented are generally not native to ENA forests. Woody species compose less than 10% of the 270 invasive nonnative plants in China.[20] Only four woody species (*Acacia farnesiana, Rhus typhina, Parthenocissus quinquefolia, Robinia pseudo-acacia*) were reported native to ENA, and only the latter two invade forests or forest margins. Similarly, all but 10 of the 321 naturalized plants in Korea listed in a working list compiled by H.H.M. Lee (based on Refs. 21–25) are herbaceous, and only two of the woody species are from North America (*R. pseudo-acacia* and *Amorpha fruticosa*), the majority from elsewhere in Asia. Miyawaki and Washitani[26] noted a large contribution of North American species in Japanese riparian areas (37% of the 87 species reported as invasive aliens), but all except *R. pseudo-acacia* were herbaceous. Auld *et al.*[27] noted the overall lack of woody or forest invaders in Japan, including those present that have not reached the same degree of invasiveness as seen elsewhere, such as southeastern Australia. Finally, Kozhevnikov and Kozhevnikova[28] listed only 21 woody species (3%) among an overall list of 676 nonnative species of the Russian Far East, and only five from ENA, including *Acer negundo, R. pseudo-acacia, Fraxinus pennsylvanica, Populus deltoides,* and *Parthenocissus inserta (vitacea)*.

In Europe, the restriction of invaders from ENA to particular habitats appears less extreme, although still biased toward the Asteraceae. One of the best characterized nonnative European floras is that of the Czech Republic,[29] which includes 1385 nonnative taxa, 90 of which are classified as invasive. The 30 invaders from ENA in the Czech Republic are a nearly even mix of annuals, herbaceous perennials, and woody species, with half of the herbaceous species represented by the Asteraceae; indeed, ENA accounts for about half of the invasive asteraceous species in the Czech flora, including many of the above meadow species that are invasive in East Asia. ENA woody species invasive in the Czech Republic also include most of those invasive in East Asia, plus *Prunus serotina*, a high-impact species that has spread throughout much of Europe.[30] Woody invaders overall, however, make up a relatively minor component of the nonnative Czech flora (17 species), and are represented by only one East Asian species (*Ailanthus altissima*). The large pool of East Asian woody invaders in ENA, particularly forest shrubs, appears to be absent from Europe, although other recent nonnative species inventories suggest their influence may be growing (e.g., in Italy,[31] where ENA composites are similarly invasive). Nevertheless, the biogeography of forest invasions in Europe and ENA seems distinct, with an Asian bias in ENA that is absent in Europe.

Development of Northern Hemisphere floras from the paleorecord

The apparent bias in modern biotic exchanges between Northern Hemisphere floras, particularly at the habitat level, invites speculation as to whether such biases can be linked to the contrasting evolutionary histories of the floras of each region. Until the mid to late Miocene (around 16–5 million years ago (Ma)), these regions and most of the Northern Hemisphere were united in a warm-temperate evergreen broadleaf and mixed forest—the Arctotertiary Geoflora[32]—with regions sharing strong climatic and taxonomic affinities.[33,34] Plant lineages across regions were shared through repeated colonization across both Beringia (until 5.5 Ma) and the North Atlantic Land Bridge (until around 15 Ma).[35] The Geoflora was progressively broken up by mid-continent aridification and cooling in the polar regions, with savanna and grassland expanding into the interior of Asia and North America between 12 and 5 Ma.[35,36] By the start of the Pliocene,

evergreen broadleaf forests resembling those of the present southeastern United States were greatly contracted in ENA but remained well distributed in Europe and East Asia, leading to greater taxonomic similarity between the Old World regions than between them and ENA.[37] During the Pliocene, ENA was instead dominated by open habitats (savanna, grassland, shrubland, parklands) increasing in openness toward the continental interior, with coniferous forests in the Southeast, a small area of mixed forest in the mid-Atlantic region, and temperate deciduous forest confined to high latitudes.[37]

During the Pleistocene, ENA experienced repeated climate fluctuations that were harsher and more rapid than those of Europe or East Asia,[38,39] potentially exacerbating the open quality of ENA habitat types. By the Last Glacial Maximum (about 18,000 years ago), Adams and Faure[40] suggested that ENA below the glacial boundary was dominated by open conifer forests well into the continental interior and down to nearly the southern coast.[41–43] In contrast, Europe was largely steppe tundra and East Asia a mix of tundra, grassland, open temperate forest, and mesic broadleaf forest further south.[40,42,44–46] By 9000 years ago, however, most of ENA, Europe, and temperate East Asia had converged on closed canopy forests, with a more tropical element in East Asia that remains today.

Broadly interpreted, reconstructions of vegetation changes across the Northern Hemisphere since the time of a united geoflora in the late Miocene suggest major differences in the recent evolutionary history of modern ENA, European, and East Asian floras.[33] These can be summarized as (1) greater divergence toward open woodland or parkland vegetation in ENA during the Pliocene compared to the forests of Europe and East Asia,[37] which was likely maintained through multiple glaciation episodes in the Pleistocene;[40] (2) greater similarity of European vegetation to that of East Asia over the Pliocene, followed by large Pleistocene climatic disruptions across Europe that greatly expanded the extent of tundra at the expense of closed forests;[42] and (3) relative continuity of forest cover across temperate and subtropical latitudes in East Asia throughout the recent Cenozoic, with a strong connection to tropical forests throughout.[34,47,48]
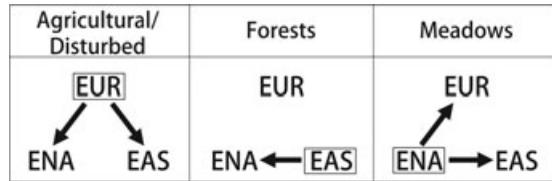

Figure 2. Apparent directionality of plant invasions for three habitat types between Europe (EUR), Eastern North America (ENA), and East/Far East Asia (EAS). Agricultural/disturbed habitats include cultivated fields, pastures, roadsides, lawns, and other systems of frequent disturbance; forests include predominantly shaded habitats during the growing season; and meadows include persistent, relatively undisturbed open habitats of rich substrate.

The case for preadaptation in the modern exchange of Northern Hemisphere floras

If a species is successful in an introduced ecosystem because it is a more effective competitor for scarce resources, and its competitive advantage stems from morphological or physiological novelties that evolved in its home range but not in the native flora, then that species can be said to be preadapted,[5] and the mechanism of invasion one of preadaptation or evolutionary innovation.[49] Conifers from Western North America, for example, are invasive at high elevations in the Southern Hemisphere because the Gondwanan flora is thought to be depauperate in frost-adapted trees due to its isolated history and low historical incidence of cold environments.[50] In the same way, one can ask whether the apparent bias in habitat exchanges across plant communities in the Northern Hemisphere may stem from differences in the evolutionary histories of their respective floras. I have summarized the major patterns of invasiveness by plants in each region and habitat (Fig. 2), and further outlined broad differences in the evolutionary history of each flora. Here, I tie these together and speculate whether a case can be made for preadaptation as a significant driver of Northern Hemisphere plant invasions. These observations are merely hypotheses; additional experimental work, such as home-and-away field comparisons of the competitive abilities and resource-use efficiencies of natives and invaders, is required for substantive development of the preadaptation invasion framework.

Why do European species dominate disturbed habitats?

The least contentious argument to be made concerning invasion through preadaptation is the case of European species in ecosystems that have been heavily modified by agricultural practices that originated in the Near East some 10,000 years ago and spread throughout Europe over the next few millennia.[19, 51] Indeed, the wholesale movement of an entire ecosystem, including forest clearance for annual cereal cultivation and pasture as Europeans colonized much of the temperate world from the 16th century onward, is a dominant theme of environmental history.[52, 53] In contrast to Europe, where cultivation-based landscapes have been common for several millennia, deforested landscapes of regular disturbance through tilling, grazing, and mowing have only been present in the Eastern United States for a few centuries.[54] It should come as no surprise, then, that few ENA natives have the innate biology to compete with Mediterranean and central European species in what are, for ENA, novel ecosystems: pastures, roadsides, lawns, cultivated ground, etc.,[8, 10, 19] just as is the case for other such transformed regions (e.g., annual invaders in the New Zealand flora).[5] This was apparent to even the earliest botanists in ENA.[9] Particularly interesting is the apparent lack of quality pasture forage in ENA, which may be due in part to a relatively short growing season for many native grasses and forbs compared to many Eurasian species[12] and the lack of dominant native grazers in ENA, at least during the Holocene.[55] Botanists and plant ecologists in the Eastern United States are familiar with the dearth of native species in chronically disturbed places; this seems more a comment on our cultural history than something in need of ecological explanation.

Why do East Asian and Russian Far East species dominate ENA forested habitats?

The large bias of species introduced from East Asia as invaders of forests of the Eastern United States must stem in part from the large number of species that have been introduced ornamentally from China, Korea, and Japan.[13] However, even given this bias, plants from this region are far more likely to be invasive than woody plants from other regions, including Europe.[8] The majority of the species in question are shrubs and vines, typically fully to partly shade tolerant,[56] and with only a few exceptions present

at the genus level in the native ENA flora.[57] Why should East Asian species be particularly good at invading ENA forests?

Fridley[57] suggested that the long evolutionary history of diverse lineages in closed forests in East Asia may have led to more effective strategies for resource capture in an understory environment—that is, the invaders are inherently better understory competitors than most of the native ENA species. One strategy in particular—the maintenance of carbon acquisition well after canopy leaf fall in autumn—was shown to be systematically greater for nonnative forest invaders compared to native species, even within the same genus.[57] The autumn advantage was not specific to East Asian species, however, and other studies have found physiological and demographic advantages for both Asian and European species versus native ENA species.[58, 59] In a specific comparison of the functional properties of East Asian and ENA species, Heberling and Fridley[60] found advantages for East Asian species for some, but not all, metabolic cost–benefit relationships. Ongoing research continues to find important physiological differences between native and invasive forest species in ENA (Fridley, Heberling, Jo, unpublished data), but such advantages do not appear to be restricted to East Asian species.

Importantly, any preadaptation argument for the East Asian bias in woody invaders in ENA must further explain why, thus far, these species appear to have limited invasion potential in the forests of Europe, despite the fact that European forests are clearly invasible.[61] Moreover, European forests typically have lower woody diversity than those of similar climates in ENA,[62] and East Asian species may be less likely to encounter ecologically similar relatives in Europe than in ENA.[57] One possibility is that invaders benefit more from the presence of earthworms in ENA, which have coevolved with both East Asian and European plant lineages but were largely absent from much of ENA until recent introductions.[63] In this case, East Asian species may be less competitively advantaged against European species that also experienced a long association with the rhizospheric effects of earthworms.[64]

Why do ENA composites spread throughout Northern Hemisphere meadows?

The largest contribution of the ENA flora to the invasive floras of Europe and Asia is its composite

(Asteraceae) flora, including perennial species common to seminatural meadows of open sites (e.g., *Solidago altissima*) and partly shaded, mesic locations (e.g., *Ageratina altissima*, *Rudbeckia laciniata*, *Symphyotrichum lanceolatum*), as well as erect annuals capable of creating large monocultures after disturbance (e.g., *Ambrosia artemisiifolia*, *Conyza canadensis*, *Erigeron annuus*, *Helianthus annuus*). It is notable that nearly all the species in question are tall, fast-growing, drought-intolerant, and often found in relatively fertile locations, particularly bottomlands, with the annuals favored in more open sites.[65,66] These are not deep forest species,[67] nor do they seem particularly tolerant to defoliation or low nutrient availability. In a classification of plant strategies, they fit the competitor or competitive ruderal mode, common to plants in temperate ecosystems of occasional disturbance and abundant resources, including meadows and riparian areas.[68] Such ecosystems tend to be on relatively nutrient-rich, geologically young substrate.[69]

It is intriguing that these are likely the conditions commonly experienced by the ENA flora over the past several million years, inhabiting a region that may have been dominated by open woodlands since the Pliocene[37] and subject to repeated soil nutrient enrichment from Pleistocene glaciations, at least over its northern half.[70] Given the richness of native ENA taxa, including composites, that dominate such habitats today, it is compelling to speculate where this group of species would have persisted in ENA during recent evolutionary time if ENA had instead been dominated by closed forests.[67] Marks[71] concluded that many of the same species in question—including *A. artemisiifolia*, *C.(Erigeron) canadensis*, and *S. altissima*—likely evolved in persistent open habitats rather than ephemeral forest gaps, in part because these species are generally less well-dispersed than those more typical of frequently disturbed habitats today. Although difficult to test formally due to the speculative nature of reconstructing past habitat conditions, if ENA experienced a greater frequency of meadow- or parkland-type vegetation than Europe or East Asia over the past several million years, it could explain both the bias in Asteraceae in mesic-temperate North America and the tendency of some of these species to invade similar habitats across the Northern Hemisphere.

Conclusion

I have drawn a portrait of modern floristic exchanges between regions of the Northern Hemisphere that emphasizes geographic directionality and habitat specificity, and have suggested that these patterns are partly the result of evolutionary processes that have occurred over millions of years in response to large-scale shifts in climate, soil conditions, and disturbance regimes. Although my intention is to elevate the status of preadaptation as a mechanism of biological invasion, this does not deny the importance of other, more proximate ecological mechanisms, including biotic resistance (whether more diverse ecosystems are less invasible) or enemy release (whether species become invasive by escaping their native predators or pathogens), which could be contributing factors in certain cases. It is further important to acknowledge the critical role played by local cultural factors, particularly land use and introduction effort, in the spread of invasive species. However, I note that mechanisms that only invoke local processes, without considering a larger biogeographic or evolutionary context, cannot explain large biases in the directionality of invasions between global biotic regions (in addition to those listed here, consider imbalances in plant exchanges to and from oceanic islands, New Zealand, between the Northern and Southern Hemispheres [as even noted by Darwin[72]], and between the major Mediterranean regions, among many such examples). Vastly different rates of biotic exchange between regions, even after accounting for differences in introduction rates, strongly point to invasion mechanisms that are evolutionary in nature, reflecting a global imbalance in the extent to which certain plant and animal lineages are adapted to modern ecosystems. Insights into how adaptive evolution has shaped the floristic composition of past and present habitats are likely to be key tools for predicting how the biosphere itself will evolve in the coming decades.

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Conflicts of interest

The author has no conflicts of interest.

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