Of Asian Forests and European Fields: Eastern U.S. Plant Invasions in a Global Floristic Context

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Abstract

Background: Biogeographic patterns of species invasions hold important clues to solving the recalcitrant ‘who’, ‘where’, and ‘why’ questions of invasion biology, but the few existing studies make no attempt to distinguish alien floras (all non-native occurrences) from invasive floras (rapidly spreading species of significant management concern), nor have invasion biologists asked whether particular habitats are consistently invaded by species from particular regions.

Methodology/Principal Findings: Here I describe the native floristic provenances of the 2629 alien plant taxa of the Eastern Deciduous Forest of the Eastern U.S. (EUS), and contrast these to the subset of 449 taxa that EUS management agencies have labeled ‘invasive’. Although EUS alien plants come from all global floristic regions, nearly half (45%) have native ranges that include central and northern Europe or the Mediterranean (39%). In contrast, EUS invasive species are most likely to come from East Asia (29%), a pattern that is magnified when the invasive pool is restricted to species that are native to a single floristic region (25% from East Asia, compared to only 11% from northerncentral Europe and 2% from the Mediterranean). Moreover, East Asian invaders are mostly woody (56%, compared to just 23% of the total alien flora) and are significantly more likely to invade intact forests and riparian areas than European species, which dominate managed or disturbed ecosystems.

Conclusions/Significance: These patterns suggest that the often-invoked ‘imperialist dogma’ view of global invasions equating invasion events with the spread of European colonialism is at best a restricted framework for invasion in disturbed ecosystems. This view must be superseded by a biogeographic invasion theory that is explicitly habitat-specific and can explain why particular world biotas tend to dominate particular environments.

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Introduction

Throughout history, plant and animal assemblages have evolved in isolated biotas that have occasionally come into contact with one another, and the resulting interchange has usually been the near-wholesale replacement of one region’s species with another’s [1–4]. Modern, human-assisted plant invasions are a clear analogue of historical biotic interchanges [3,5], and yet relatively few invasion biologists have asked whether there are regular patterns of global dominance of plants from particular floristic regions [6,7]. If such patterns exist, they would be of prime importance to the management community concerned with invasions, as resources for prevention and control could be focused on those regions most likely to be sources of future invaders [8]. Such patterns would also be a significant advance for ecologists and evolutionary biologists still struggling to identify generalizations concerning which plants invade [9,10,11] and which communities are most susceptible to invasion [12–15].

The Eastern U.S. (EUS) has seen an unprecedented spread of invasive species in nearly all major habitats over the past century [16,17], and these non-native species represent nearly all of the world’s floristic regions. The diversity of invader habitats and their provenances includes the turfgrass pest Poa annua (annual bluegrass, from Europe); the mesic forest understory grass Microstegium vimineum (Japanese stiltgrass, from southeast Asia); the floating freshwater aquatic Eichhornia crassipes (water hyacinth, from the Amazon basin); many fast-spreading shrubs of open, disturbed woodlands such as Lonicera tatarica (Tartarian honeysuckle, from the steps of central Asia); major crop pests like Cynodon dactylon (purple nut sedge, probably from India); and canopy dominants that threaten to replace entire forest stands such as Triadica sebifera (Chinese tallow tree). Is there any underlying pattern to which global floras contribute invaders to particular habitats? Are the provenances of those species that become invasive an unbiased subset of total alien flora, or are invaders more likely to come from particular evolutionary centers of origin?

To invade, a species must be introduced, establish, and spread [18], and processes specific to each of these stages could bias non-native floras toward particular provenances. For example, introduction attempts of non-native species to a focal region may vary according to geographic origin due to historical differences in rates of trade and travel between regions [19]. Furthermore, introduced species that become naturalized should preferentially come from areas that match certain climate, soil, or disturbance conditions that allow a species to reproduce without human assistance [20]. Finally, on top of floristic biases in both
introduction attempts and naturalizations, species that become invasive—those that spread naturally and compete successfully with native vegetation—may preferentially come from certain regions where species have achieved superior levels of fitness under competition in a given environment, what Darwin [1] referred to as a “higher stage of perfection or dominating power”, and others have referred to as ‘preadaptation’ [21]. This hierarchy based on different mechanisms of introduction, establishment, and spread suggests that comparing floristic patterns of different components of non-native floras (e.g., the provenances of alien species versus the subset of those that become invasive) could help refine studies of biological attributes that allow a typically small subset of introduced species to become invasive. The hierarchy also suggests that non-native floristic associations should vary strongly by habitat type [3,9,22,23], given 1) modes of introduction vary by habitat type, as accidental introductions are often agronomic and follow the spread of agricultural operations, whereas ornamental introductions span a larger range of potential environments (sun versus shade, xeric versus mesic); 2) global floristic regions vary greatly in habitat representation, and some floras lack major habitat types entirely (there is no mesic deciduous forest in the Sahara); and 3) superior competitive abilities are more important to invader success in some habitats, particularly those of low disturbance intensities [24,25].

In this paper I analyze the alien and invasive vascular floras of the EUS coincident with the Eastern Deciduous Forest biome of North America [26] to determine whether alien and invasive plant species of this region are more likely to come from particular source floras, using the Takhtajan [27] global floristic regions as source areas that correspond to global centers of plant diversification (Fig. 1). Due to the prevailing view that strategies for plant success depend strongly on habitat qualities, which in turn suggests that global floras should preferentially contribute species to certain habitats, I conducted the analysis for invasive species using a habitat classification (Table 1) based on environmental differences that select for well known differences in plant strategies (disturbance regime and resource availability [25]). Two plant strategies associated with habitat type that are widely available for floristic-based analyses include species growth form (trees, forbs, etc.) and duration (annual, biennial, perennial); for these attributes I also asked whether native, alien, and invasive components of the EUS flora exhibit regular differences in attribute composition associated with floristic and habitat patterns. The primary objective of this study was to address whether modern plant invasions are qualitatively any different from biotic interchanges throughout the history of biotic migrations [4,5,28]—that is, whether biogeographic patterns of modern invasions reveal new evolutionary-based insights that provide a general framework for predicting where invaders come from and which areas are preferentially invaded.

Results

The alien flora of the EUS includes 2629 vascular plant taxa, 449 of which (17%) are documented as invasive (Table 2). Infra-specific taxa (subspecies and varieties) account for 304 of the alien taxa and 14 of the invasive taxa. Alien taxa of the EUS come from all major global floristic zones (Table 2). Nearly half (45%) of the alien taxa have native ranges that overlap the Circumboreal floristic region (including central and northern Europe; Fig. 1), followed in representation by the Mediterranean (39%), Irano-Turanian (31%), and Eastern Asiatic (24%) regions. Of the world floristic regions where nativity could be reliably assigned, the Neozeylandic region is the smallest donor to the EUS alien flora (7%), and 5% of the alien taxa are derived from cultivation (many crops and ornamental plants). Of the 2629 taxa analyzed here, about 50 could not be reliably categorized into native floristic regions, due to lacking nativity information, highly questionable non-native status, or native-non-native hybrid origin; eight of these were reported invasive (see Supplemental Dataset S1).

The subset of 449 invasive EUS taxa is not a random sample of native floristic regions of the alien taxa (Table 2, Fig. 2). Twenty-nine percent of the alien taxa with native ranges that include the Eastern Asiatic region are reported invasive, compared to 22% and 20% of the alien taxa from Circumboreal and Mediterranean regions. Alien taxa present in the Sahara-Arabian and Irano-Turanian regions also include high proportions of invasive taxa (42% and 27%, respectively). However, when alien taxa were instead restricted to those that only occur in a single native region (region endemics), the amount of invasive taxa from Sahara-Arabian and Irano-Turanian regions essentially disappeared (0%).

Figure 1. Floristic regions of the world, from Takhtajan [27]. Region names and associated statistics are listed in Tables 2 and 3. Those shown here do not include several largely oceanic or archipelagic regions ignored in the present analysis.
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and 3%, resp.), as did those from the Mediterranean (2%). This in part reflects the clear relationship between native range size, measured as the number of floristic regions inhabited, and invasion potential (Fig. 3). Despite the smaller overall invasive proportion of region-endemic alien taxa (13%; Table 2), endemics from East Asia have nearly as high an invasive percentage as non-endemics (25%), whereas the percentage of endemic invaders from the Circumboreal region is cut in half (11%, compared to 22% non-endemic invaders). The Neozelandic region is the only region to lack any invasive contribution to the EUS flora.

A majority of the invasive flora (74%) is found in open habitats of irregular disturbance, followed by roadsides (44%), managed

| Table 1. Habitat classes describing the environmental associations of plant invaders of the Eastern U.S. |
|-----------------------------------------------------------------------------------------------|
| **Habitat** | **Description** |
|-------------|-----------------|
| Aquatic     | Floating or submerged vegetation, in ponds, impoundments, lakes, or streams. |
| Forest      | Habitats characterized by significant tree canopy cover, including woodlots, forests, suburban woodlands, open woodlands, disturbed forest, riverine woods, old homesites, wet forests, swamps, forested bottomlands, dry woodlands, ridgetop woods. |
| Managed     | Unshaded habitat that is the product of continuing disturbance (annual or frequent basis), including agricultural systems (of turf, alfalfa, or other annual crops), pasture, rangeland, plantations, lawn, barnyards, gardens, cropland. |
| Open        | Unshaded, early successional habitats that are the product of past or irregular natural or anthropogenic disturbance, including thicketse, waste places, disturbed areas, old fields, sandy shores, hedgerows, fencelands, woodland edges, wood borders, fields, trails, urban lots, dunes, coastal sands, meadows. |
| Riparian    | Habitats associated with flowing water, including riparian, streamside, stream banks, river banks, gravel bars, riverine forest, bottomland, floodplains, riverine woods, rivers, floodplain forest. |
| Roadside    | Frequently disturbed habitat associated with transport, including roadsides, road banks, road ditches, right of ways, railroad embankments. |
| Wetland     | Seasonally or continually wet terrestrial habitats, including wetland, seeps, ditches, bogs, marshes, lowlands, waterways. |

Each invasive species was assigned to one or more classes based on habitat descriptions listed in major Eastern U.S. floras [52–54].

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| Table 2. Eastern U.S. alien and invasive floras categorized by global donor floristic regions [27]. |
|-----------------------------------------------------------------------------------------------|
| **Region** | **Region Name** | **Alien taxa** | **Invasive taxa** | **% Invasive** | **Alien taxa (region endemics)** | **Invasive taxa (region endemics)** | **% Invasive (region endemics)** |
|------------|-----------------|----------------|------------------|---------------|---------------------|---------------------|-----------------------|
| 1          | Circumboreal    | 1196           | 266              | 22%           | 282                 | 31                  | 11%                   |
| 2          | Eastern Asiatic | 622            | 180              | 29%           | 291                 | 74                  | 25%                   |
| 5          | Macronesian     | 303            | 53               | 17%           | 1                   | 0                   | 0%                    |
| 6          | Mediterraneian  | 1027           | 205              | 20%           | 143                 | 3                   | 2%                    |
| 7          | Saharo-Arabian  | 105            | 44               | 42%           | 1                   | 0                   | 0%                    |
| 8          | Irano-Turanian  | 815            | 220              | 27%           | 68                  | 2                   | 3%                    |
| 9          | Madrean         | 42             | 8                | 19%           | 14                  | 3                   | 21%                   |
| 10         | Guineo-Congolian| 93             | 11               | 12%           | 1                   | 0                   | 0%                    |
| 11,13,28   | [South African] | 92             | 8                | 9%            | 6                   | 0                   | 0%                    |
| 12         | Sudano-Zambesian| 189            | 20               | 11%           | 13                  | 0                   | 0%                    |
| 15         | Madagascan      | 52             | 6                | 12%           | 1                   | 0                   | 0%                    |
| 16         | Indian          | 147            | 26               | 18%           | 12                  | 2                   | 17%                   |
| 17         | Indo-Chinese    | 153            | 28               | 18%           | 4                   | 2                   | 50%                   |
| 18         | Malesian        | 149            | 22               | 15%           | 1                   | 0                   | 0%                    |
| 23         | Caribbean       | 96             | 9                | 9%            | 18                  | 1                   | 6%                    |
| 25         | Amazonian       | 66             | 10               | 15%           | 3                   | 1                   | 33%                   |
| 26         | Brazilian       | 157            | 14               | 9%            | 22                  | 2                   | 9%                    |
| 27         | Andean          | 99             | 8                | 8%            | 13                  | 0                   | 0%                    |
| 29,30,31   | [Australian]    | 103            | 9                | 9%            | 10                  | 0                   | 0%                    |
| 33         | Chile-Patagonian| 132            | 11               | 8%            | 20                  | 2                   | 10%                   |
| 35         | Neozelandic     | 7              | 0                | 0%            | 1                   | 0                   | 0%                    |
| [Cultivation origin] | 141 | 9 | 6% | NA | NA | NA |
| All Regions | 2629           | 449            | 17%              | 925           | 123                 | 13%                 |

Floristic regions refer to Fig. 1. Each region is listed with its contribution to the total alien and invasive flora of the Eastern U.S. Region endemics are those taxa native to a single floristic region.

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(annually disturbed) ecosystems (34%), forests (29%), and wetland, riparian, and aquatic systems (13%, 13%, and 4%, respectively; Table 3). More than half of the woody invasive taxa (58%) are from the Eastern Asiatic region, and significantly more of the East Asian taxa (56%) are woody than expected based on the overall representation of woody invaders. At the other extreme, the invaders of four regions were significantly more likely to be herbaceous than the overall invasive pool, including those from the Sudano-Zambezian (100% herbaceous), Macronesian (96%), Saharo-Arabian (86%), and Mediterranean regions (80%; all \( P < 0.05 \); Table 3).

Several regions exhibited significant habitat bias in their invasive representation (Table 3, Fig. 2). Annually disturbed, managed ecosystems are far more prone to invasion from Mediterranean plants than plants from the Eastern Asiatic region (\( P < 0.001 \); Fig. 2). Conversely, 41% (74/180) of the invasive taxa from East Asia invade forests, compared to only 7% (4/53) invaders from Macronesia and 29% of the invasive taxa overall (Table 3). Significant deviations in habitat representation among invaders from different source floras also include a greater representation of East Asian taxa in riparian habitats and very few Irano-Turanian species in aquatic habitats (Table 3). Major floristic patterns of the invasive pool of all habitat types are illustrated in Fig. 2.

The composition of species growth form and duration is significantly different among native, alien, and invasive EUS floras, with departures being greatest between the invasive and alien pools (Table 4). Compared to the native flora, the alien flora is overrepresented by annuals, biennials, and vines, and under-represented by shrubs and grasses. Other growth form categories have remarkably similar representation in the native and alien floras, including the overall split between woody and herbaceous taxa (about 1 woody species in 5). In contrast, the growth form and duration composition of the invasive flora shows a strong departure from the alien flora. Invaders were significantly more likely to be perennial trees, shrubs, and vines, and thus much less likely to be herbaceous (65%) than both the native or alien floras (Table 4).
Discussion

The typical alien vascular plant of the Eastern Deciduous Forest biome of the Eastern U.S. is a European forb, either from the Circumboreal northern and central regions of Europe or the southern Mediterranean region. The clear European bias in non-native plants has been documented in many global floras by plant biogeographers [6,7,29] and ecological historians [30,31] and is referred to as the Imperialist Dogma [30]. This model asserts that the ancestral cradle of plant invasions is only useful in so far as it describes the recent co-evolution of ‘weedy’ plants in historically novel human-dominated ecosystems [32]—a restricted set of conditions when viewed in the full context of plant invasions in a variety of disturbed and natural ecosystems worldwide.

In contrast to the total alien flora, EUS alien invaders are commonly woody species from East Asia, perhaps better reflecting EUS landscapes as dominated by closed secondary forests. Indeed, the composition of the alien flora is used as a null model for invader composition, taxa from some regions are significantly more likely to invade (Table 2). It should come as no surprise that invasive taxa are most likely to come from areas with climates that resemble those of EUS (Fig. 1)—all floristic regions of greater-than-expected invader representation (visualized in Fig. 3). This is particularly true of the high invader contribution of more arid

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**Table 3.** Habitats and growth forms that characterize the invasive plant species from each global donor floristic region.

| Region | Region Name | Open | Managed | Forest | Wetland | Roadside | Riparian | Aquatic | Woody | % Woody invaders |
|--------|-------------|------|---------|--------|---------|----------|----------|---------|-------|-----------------|
| 1      | Circumboreal | 208  | 113     | 61     | 27      | 132      | 28       | 11      | 70    | 203 26%         |
| 2      | Eastern Asiatic | 126  | 36***   | 74***  | 27      | 72       | 32*      | 6       | 101*** 90 56%   |
| 5      | Macaronesian | 46   | 23      | 4**    | 6       | 31       | 3        | 3       | 2     | 51*** 4%        |
| 6      | Mediterranean | 166  | 100***  | 42     | 24      | 105      | 23       | 9       | 41    | 169*** 20%      |
| 7      | Saharo-Arabian | 36   | 22      | 7      | 4       | 25       | 2        | 4       | 6     | 39** 14%        |
| 8      | Irano-Turanian | 180  | 89      | 58     | 26      | 114      | 29       | 6*      | 64    | 164 29%         |
| 9      | Madrean       | 8    | 6       | 0      | 0       | 6        | 0        | 0       | 1     | 8 13%           |
| 10     | Guineo-Congolian | 8   | 6       | 1      | 2       | 5        | 1        | 1       | 0     | 11 0%           |
| 11,13,28 | [South African] | 3    | 2       | 0      | 1       | 3        | 1        | 1       | 0     | 8 0%            |
| 12     | Sudano-Zambezian | 14  | 8       | 1      | 4       | 10       | 4        | 2       | 0     | 20*** 0%        |
| 15     | Madagascan    | 4    | 3       | 0      | 0       | 4        | 0        | 1       | 0     | 6 0%            |
| 16     | Indian        | 22   | 9       | 8      | 8       | 11       | 7        | 1       | 6     | 21 23%          |
| 17     | Indo-Chinese  | 19   | 6       | 9      | 6       | 14       | 4        | 1       | 10    | 19 36%          |
| 18     | Malesian      | 19   | 7       | 7      | 5       | 13       | 5        | 0       | 6     | 17 27%          |
| 23     | Caribbean     | 7    | 3       | 1      | 0       | 4        | 0        | 1       | 3     | 8 33%           |
| 25     | Amazonian     | 6    | 2       | 0      | 1       | 1        | 0        | 4       | 3     | 9 30%           |
| 26     | Brazilian     | 9    | 3       | 0      | 2       | 4        | 0        | 4       | 6     | 11 43%          |
| 27     | Andean        | 6    | 2       | 0      | 0       | 3        | 0        | 2       | 3     | 7 38%           |
| 29,30,31 | [Australian]  | 7    | 1       | 3      | 3       | 4        | 3        | 1       | 4     | 7 44%           |
| 33     | Chile-Patagonian | 6   | 4       | 0      | 1       | 4        | 0        | 3       | 4     | 9 36%           |
| 35     | Neozeylandic  | 0    | 0       | 0      | 0       | 0        | 0        | 0       | 0     | 0 0%            |
| All Regions | 334  | 153    | 129    | 59     | 197      | 58       | 19      | 175   | 293 39%        |

Floristic regions refer to Fig. 1. Bold counts are statistically significant outliers in Pearson chi-square analysis with significance level indicated by asterisks (overall habitat x region χ² = 243.6 on 120 df; P < 0.001; growth-form x region χ² = 104.1 on 20 df; P < 0.001; *P < 0.05; **P < 0.01; ***P < 0.001.

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Table 3. Habitats and growth forms that characterize the invasive plant species from each global donor floristic region.
temperate regions (including the Saharo-Arabian, Irano-Turani-an, and Mediterranean)—regions with almost no EUS invaders endemic to them. Of particular interest is that, although overall those alien taxa endemic to particular floristic regions are very unlikely to be invaders (13%), those endemic to East Asia are nearly as invasive as the entire invader pool from East Asia (25% compared to 29%). Of those other regions with at least 20 EUS alien taxa that are natively endemic, only two—the Circumboreal and Chile-Patagonian regions—have at least 1 in 10 of those as invasive (11% and 10%, respectively), despite similar climates to the EUS existing on all continents [34].

Why is the flora—and in particular the woody forest flora—of East Asia so unusually invasive in the Eastern U.S.? From a broad historical perspective, colonization of EUS mesic forest habitat by East Asian plants is hardly novel. The late Pleistocene origin of the Eastern Deciduous Forest is thought largely to stem from the southern Appalachians and adjacent Cumberland Plateau [26,35], and floristic similarities between this region and the forests of Japan and central China have been of great interest to botanists for centuries [36,37]. These regions were connected via Beringia for much of the Tertiary, and taxonomic disjunctions, largely at the genus level, have resulted from periods of isolation following continental drift, increasing aridity in the Western U.S., and cool and dry conditions associated with major glaciation events in EUS [38,39]. Interestingly, White [38] found these disjunct genera to be overrepresented by woody understory taxa, similar to the qualities of overrepresented invasive taxa reported here. Furthermore, most of the major woody forest EUS invaders endemic to East Asia have congeners in the EUS native flora, including Berberis thunbergii (native is B. canadensis), Celastrus orbiculatus (near-endemic to East Asia, native is C. scandens), Elaeagnus umbellata (E. commutata), Elaeagnus alatus (several native bush Euonymus), Lupinus mollisus (L. canadensis), Rosa multiflora (several natives), Viburnum dilatatum (several natives), and Wisteria sinensis (W. floribunda), among others. It is therefore tempting to suggest that the modern invasion of EUS forests is only the latest chapter in a long history of highly (pre)adapted Asian lineages colonizing mesic temperate forests worldwide. Consistent with this view, few if any woody understory species from EUS (or Europe) made a list of 126 non-native plant species in China [40]. If true, it suggests that forest invasion mechanisms can be deconstructed by comparative ecophysiological studies of East Asian-EUS sister taxa. It also qualitatively supports patterns of biotic interchanges throughout geologic history, in that modern invasions are similarly characterized by certain regions donating more invaders to particular habitats [2].

An important component of invasive species management is the prevention or early detection of species that exhibit strong invasive tendencies [41], and the association of invaders from certain regions with particular habitats (Fig. 2) suggests several guidelines for natural area management in the EUS. First, although the European bias in alien species persists for those invaders of open and managed habitats, European species are significantly less likely to pose significant management concern in forested natural areas of the Eastern U.S. Instead, managers should be particularly concerned about current and future introductions of woody plants from East Asia that already account for the majority of woody species that dominate forest understories. Second, native endemism can be an important tool for screening plant invasive potential. It is already well appreciated that species of larger native ranges are more likely to become pests in their introduced range [11,42]; the present study confirms this and adds greater detail by classifying endemism according to specific regions. For example, although a significant number of EUS invaders are sub-Saharan African in origin (particularly warm-season grasses), there is not a single EUS invader endemic to an African floristic region (Table 2).

On the other hand, there are only four EUS alien taxa endemic to the Indo-Chinese region of southeast Asia, and yet two of these are invasive, again attesting to the strong invasive potential of Asian taxa in the Eastern U.S. Finally, the strong bias toward woody plants in the invasive pool (39%) compared to the alien (23%) or native florae (24%), despite many invasive lists being derived from agricultural activities where woody species are less common, suggests conservationists and natural resource managers in the EUS focus energies on preventing the introduction and local establishment of non-native woody species [17,43]. It is also important to consider that many alien species only become invasive after significant time lags [44], suggesting that Asian woody taxa considered non-invasive in the present study nonetheless be treated carefully in horticultural practice.

The clear floristic distinction between alien and invasive plant taxa in the EUS, and the strong biases in habitat representation between invaders of different origin and life history attributes, is further rationale for more careful delimitation of the focal species pool in invasion studies [23]. In particular, the failure of plant ecologists to identify easily screened attributes of ‘invaders’ should be expected if analyses include all alien (non-native, exotic) taxa [45]. Species that successfully naturalize do share attributes relating to long-distance dispersal ability and reproductive potential [7,10,11], but the present study suggests critical attributes of those that become invasive are specific to particular environmental circumstances rather than universal across habitat types. If other global regions show floristic biases in the invasive species pools of particular habitats that resemble those described in the present study, there should be renewed motivation for comparative studies of the biology of plants from different florae. As modern invasions increasingly appear to qualitatively resemble past biotic interchanges [3,4,5], such comparative studies may also help paleobiologists better understand the historical development of modern plant assemblages.

Table 4. The composition of native, alien, and invasive vascular plant floras of the Eastern U.S. with respect to growth habit and duration [46].

| Growth Form | Native flora | Alien flora | Invasive flora |
|-------------|-------------|-------------|---------------|
| # taxa %     | # taxa %    | # taxa %    |
| Trees        | 463 8%     | 243 9%     | 82*** 18%    |
| Shrubs       | 1149 21%   | 455*** 17% | 129*** 29%   |
| Vines        | 195 3%     | 177*** 7%  | 42* 9%       |
| Graminoids   | 1110 20%   | 411*** 16% | 54*** 12%    |
| Forbs        | 3436 62%   | 1720 65%   | 239*** 53%   |
| Woody        | 1330 24%   | 607 23%    | 175*** 39%   |
| Herbaceous   | 4546 82%   | 2131 81%   | 293*** 65%   |
| Annuals      | 1057 19%   | 985*** 37% | 122*** 27%   |
| Biennials    | 191 3%     | 228*** 9%  | 45 10%       |
| Perennials   | 4727 85%   | 1722*** 66%| 336** 75%    |
| Total flora  | 5574       | 2629       | 449          |

*P<0.05; **P<0.01; ***P<0.001.

Percentages are relative to the total flora counts for each group. Native flora statistics do not include infraspecific taxa or hybrids. Bold counts are statistically significant outliers in Pearson chi-square analysis, comparing the alien flora counts with the native flora, and the invasive flora counts with the alien flora. Tests were performed separately for the three classifications indicated (specific growth forms, herbaceous vs. woody, and duration).

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Materials and Methods

I constructed a database (Supplemental Dataset S1, with associated metadata in Supplemental Text S1) of all alien vascular plant taxa present in the Eastern Deciduous Forest of the Eastern U.S. (state occurrences from MN to LA, east to the coasts of ME to GA, excluding presences unique to FL) using the USDA PLANTS database [46]. I defined as alien those taxa listed as “Introduced” by USDA PLANTS residing in the above states. Taxa such as Phragmites australis with native and exotic populations listed as “Native and Introduced” were not included. I included unambiguous non-native infraspecific taxa (e.g., Taraxacum officinalis ssp. officinalis, Ranunculus acris var. acris, Viburnum opulus var. opulus) that are tracked by PLANTS. Alien plant species in the U.S. are only tracked by PLANTS if their native range is wholly outside the contiguous U.S., preventing analysis of those alien taxa native to the Western U.S. Alien plants were categorized as “invasive” if they were represented on the USDA PLANTS “Weedy and Invasive Plants” lists for Eastern U.S. regions, including the Northeast [47], Kentucky [48], Tennessee/Southeast [49], and Wisconsin [50], plus any remaining alien taxa that were indicated as present in the selected states in the WeedsUS database maintained by the U.S. National Park Service [51]. The invasive plant definition used here is thus an alien in the Eastern U.S. of significant management concern.

All species were assigned growth form and duration attributes according to the USDA PLANTS database. Growth form attributes included the non-exclusive forms “tree”, “shrub” (including “subshrub”), “vines”, “graminoid”, and “forb/herb”; “herbaceous” and “woody” classes were derived from lumping “graminoid” and “forb/herb” forms (which includes all herbaceous vines) and “tree”, “shrub”, and “vines” forms (using only those vines which were not also listed as forbs). A small set of species are semi-woody and are included in herbaceous and woody categories. Duration attributes included annual, biennial, and perennial designations. The composition of the alien flora with respect to these attributes was compared to the EUS native flora using a species-level query of contiguous U.S.-native plants residing in the above selected states from PLANTS. The subset of alien species defined as invasive was further assigned habitat designations describing the environmental circumstances of their occurrences in EUS. Detailed habitat descriptions were first obtained from major EUS floras [52,53,54]; these idiosyncratic descriptions (e.g., “wet meadows”, “bottomland hardwood forests”) were then grouped into seven habitat classes meant to describe important environmental correlates (disturbance regime, light availability, soil moisture status). Table 1 summarizes this classification, as illustrated in Fig. 2. Non-invasive alien species are typically rare in their introduced ranges, preventing any reliable assessment of foreign habitat affinity for these taxa.

All alien taxa in the EUS flora were assigned membership to native source floras using the floristic region designations of Takhtajan [27] (Fig. 1). Takhtajan’s system is based on geographic patterns of endemism, particularly at the species and genus levels, and is meant to represent patterns of historical isolation and evolutionary divergence in the global distribution of vascular plants [55]. Along with the antecedent work of Good [56], to which it closely coincides, it remains the only attempt to categorize the world’s flora phylogenetically at the sub-continental scale [55]. For studies of plant species behavior based on aspects of their evolutionary history, Takhtajan’s regions thus represent a clear advantage over native biogeographic units based on geopolitical boundaries. Each alien taxon was assigned to one or more Takhtajan regions according to documented native range descriptions from source floras. The majority of these assignments were accomplished with taxon queries in the online Germplasm Resources Information Network [57], a central location of floristic distribution information compiled from world floras. In some cases where GRIN records were unavailable, a number of other source floras were consulted. In general, the assignment of native ranges to floristic regions for those taxa distributed close to region boundaries was conservative. A list of native floristic regions for each taxon, along with additional bibliographic information, is available as Supplement Dataset S1 and Text S1. Due to small spatial resolution and sample sizes of alien taxa, three Takhtajan regions for the southern tip of Africa were combined into a single region, as were the three floristic regions of Australia (Table 2). Alien taxa were also essentially absent from small island or archipelago regions, and are ignored in the present analysis.

Contingency tables of floristic region vs. habitat and floristic region vs. growth form were analyzed for independence with Pearson chi-square tests in R [58]. Significant residuals were identified with the Freeman-Tukey deviate statistic [59], with a threshold of an expected count of at least 5 for significance [60].

Supporting Information

Dataset S1 Native floristic zones of alien plant taxa of the Eastern U.S. database.

Text S1 Native floristic zones of alien plant taxa of the Eastern U.S. database: metadata.

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Author Contributions

Analyzed the data: JDF. Contributed reagents/materials/analysis tools: JDF. Wrote the paper: JDF.

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