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Biotic interchange in the Anthropocene: strong asymmetry in East Asian and eastern North American plant invasions

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ABSTRACT

Aim Modern species invasions result in the global reshuffling of regional floras, but biogeographical biases in floristic exchanges (origin effects) are underexplored. We compared habitat-level invasion patterns in two environmentally similar regions, and ask whether plant exchanges are also similar or if one region largely invades the other.

Location Eastern North America (ENA) and East Asia (EAS).

Methods We compiled a new dataset of the 1293 naturalized (i.e. non-native, self-sustaining) and invasive (i.e. spreading) plant taxa in EAS, including the habitats they invade and their native distributions. We tested for biases by biogeographical origin, growth form and habitat in EAS invasions, and compared them with those for ENA.

Results EAS contains 51% fewer naturalizations than ENA, but with a similar biogeographical representation. However, invasions in each region show large differences in biogeographical affinity, taxonomic representation and habitat. Invasions in ENA are biased from East Asia (29% invasive), while invaders in EAS come from a fairly uniform set of major temperate regions. Taxonomically, 54% of Asteraceae naturalizations in EAS are invasive compared with only 16% in ENA. Open habitats are highly invaded in both regions (75% of invasions), but forests are significantly more invaded in ENA than EAS (29% vs. 9%). Reciprocal invasions are asymmetric: EAS contributes more woody invaders to ENA than expected (56% woody, $P < 0.001$), while in EAS nearly all (91%) invaders from ENA are herbaceous.

Main conclusions Although they represent regions of similar temperate environments, the origin, taxonomy and habitat affinities of plant invaders in EAS and ENA floristic regions are strongly contrasting. These differences are robust to differences in introduction effort when the invasiveness of species once naturalized is considered. We suggest these patterns support a historical perspective of invasions that invokes differences in regional selection pressures that pre-adapt certain floras for invasion into particular environmental conditions.

Keywords

Biological invasions, floristic interchange, invaded habitat, naturalized plants, preadaptation, reciprocal invasions.

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INTRODUCTION

The globalization of human activities has resulted in the unprecedented movement of plants around the world (van Kleunen *et al.*, 2015), resulting in novel assemblages of 'native' and naturalized species with divergent evolutionary histories (Hobbs *et al.*, 2006). Yet for any given region the subset of introduced species that are able to naturalize or invade intact communities is not random with respect to their native provenance (Buckley & Catford, 2016). Island species, for example, rarely invade continental floras (Fridley & Sax, 2014); Northern Hemisphere lineages are more invasive in similar climates in the Southern Hemisphere than vice versa (van Kleunen *et al.*, 2015); and short-lived forbs and grasses from Europe tend to dominate frequently disturbed, open habitats in temperate regions world-wide (di Castri, 1989; Fridley, 2008). This 'origin effect' is not easily explained by processes that arise in the introduced range, such as enemy release (Keane & Crawley, 2002) or rapid evolution (Blossey & Notzold, 1995), but instead suggests that historical differences in introduction effort or evolutionary processes across regions are important drivers of modern biotic exchanges (Buckley & Catford, 2016). For example, because plant invaders often show performance advantages over co-occurring native species (van Kleunen *et al.*, 2010) and successful invaders tend to have wider physiological niches (Higgins & Richardson, 2014), some researchers have suggested invaders may be 'pre-adapted' for superior competitiveness or tolerance of environmental conditions as a consequence of their evolutionary history (Vermeij, 1991, 2005; Mack, 2003; Fridley & Sax, 2014). If this is true, then it follows that biases of invader origin to a particular region should vary by habitat, and in a way consistent with the current or historical importance of a given habitat type in a potential invader's native range. The invasiveness of pines in the Southern Hemisphere, for example, is predicated in large part on species traits in the light of frequent fire (Higgins & Richardson, 1998; Grotkopp *et al.*, 2002).

In this paper, we frame an analysis of invader origin effects in the context of two environmentally similar but historically isolated temperate floras: East Asia (EAS) and eastern North America (ENA). Since the Linnaean era, botanists have recognized close phylogenetic and ecological similarities between these regions (Boufford & Spongberg, 1983). ENA and EAS share similar modern climates, soils and vegetation types, and experienced considerable floristic interchange during the Tertiary period, particularly before the Pliocene (Qian & Ricklefs, 1999; Donoghue & Smith, 2004; Fridley, 2013). Despite these similarities, a clear modern-day diversity bias exists, with EAS comprising more plant families, genera and species (Qian & Ricklefs, 1999). Within 58 disjunct plant genera, EAS has nearly twice the number of species as ENA, probably due to large-scale historical differences in extinction rates between regions rather than differences in habitat or land area alone (Guo *et al.*, 1998; Qian & Ricklefs, 2000). The greater diversity of the EAS flora was hypothesized to

have led to increased selection pressures for efficient use of resources compared with ENA (Heberling & Fridley, 2012). Indeed, analyses of naturalized species in ENA find strong biases in invasion patterns, with a large fraction of ENA invaders originating from EAS (Fridley, 2008). Further, eco-physiological comparisons in ENA indicate that EAS invaders are less constrained by metabolic tradeoffs than ENA natives (Heberling & Fridley, 2013).

If historical environmental differences translate to modern biases in invasion patterns, EAS should be less invaded than ENA (Fridley, 2011, 2013). To date, however, analysis of reciprocal EAS–ENA invasion patterns has been limited by insufficient naturalized and invasive plant lists and associated habitat information from the EAS region. The distinction of naturalized and invasive species pools is important in this context, because the former can serve as a control for differences in introduction effort between regions (Richardson & Pysek, 2012). That is, even if greater introduction effort has led to a larger naturalized (non-native, self-sustaining) species pool in a particular region, the size and composition of the subset that has become invasive (locally abundant or rapidly spreading) is a measure of invasiveness related to particular attributes (e.g. provenance, taxonomy; Fridley, 2013). Analyses based on the proportion of naturalized species that are invasive, rather than absolute numbers of naturalizations, allow for meaningful interpretation of the invasibility of a region across regions (Richardson & Pysek, 2012).

Here, we present an analysis of non-native vascular plant exchanges across ENA and EAS, compiling regional datasets for the Russian Far East, North Korea, South Korea and China. Specifically, we asked the following.

1. Do EAS invaders have similar biogeographical origins as the ENA invasive flora? That is, are non-native taxa in EAS biased toward particular global floristic regions?
2. Are similar habitats in EAS and ENA prone to invasions from the same species?
3. Are invasions between EAS and ENA asymmetrical, such that the flora of EAS contributes proportionally more to ENA than vice versa?
4. Are those lineages (plant families) that are most invasive in ENA similar to those in EAS, as would be expected if particular families are best adapted to similar environments?

METHODS

Compilation of a non-native floristic dataset

Datasets for the non-native vascular floras of EAS and ENA were compiled from various sources (described below), following the phytogeographical regions of Takhtajan (1986). EAS refers to the 'Eastern Asiatic' floristic region (Takhtajan, 1986; region 2 in Fig. 1), which encompasses temperate China, the Korean Peninsula and the Russian Far East. ENA refers to the 'North American Atlantic' floristic region (region 3, Fig. 1), which encompasses the Eastern Deciduous Forest biome of ENA. We used floristic regions rather than political units for our analysis because the former better

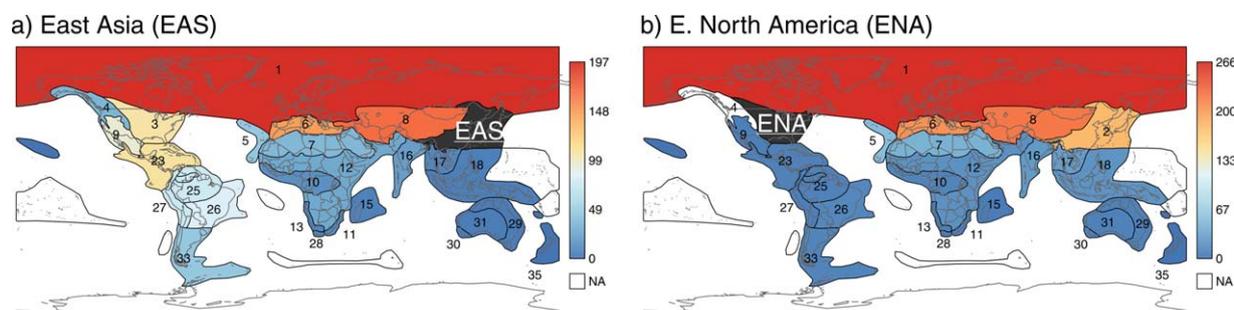


Figure 1 Number of plant invasions from each floristic region (Takhtajan 1986) in (a) East Asia and (b) Eastern North America. Numbers refer to major phytogeographical regions of Takhtajan (1986; see Table 2 for names of regions). Recipient regions are indicated by the labels 'EAS' and 'ENA'.

represent shared plant evolutionary histories (Takhtajan, 1986) in the context of our hypotheses.

To account for redundancy across regional datasets due to taxonomic synonyms, scientific names were standardized according to The Plant List (<http://www.theplantlist.org/>), using the 'Taxonstand' package (Cayuela *et al.*, 2012) in R (R Core Team, 2015). Where The Plant List did not have high confidence in synonym status, the original names in the datasets were used. Intraspecific taxa (*i.e.* varieties) were kept as separate entries in all cases where the source references treated these taxa separately. Growth form (*e.g.* graminoid, forb/herb, shrub, tree, vine) and duration (annual/perennial) were assigned according to the definitions of USDA Plants (USDA, NRCS, 2014).

Definitions of naturalized and invasive species

We followed the standardized terminology of Pysek *et al.* (2004) to categorize non-native species along the introduction–naturalization–invasion continuum (Richardson & Pysek, 2012). 'Naturalized' taxa are those introduced to a region that can sustain self-replacing populations without human intervention. 'Invasive' taxa consist of a subset of naturalized species that can reproduce and spread over a large area. The small subset of taxa that were native in one particular region but invasive elsewhere within the same region of interest (*e.g.* native to China but invasive in the Russian Far East) were excluded from the analyses but are included in Appendix S1 in the Supporting Information.

ENA naturalized flora

We utilized a previously published dataset of the non-native vascular plant taxa in ENA (Fridley, 2008), which was constructed using the USDA PLANTS database (USDA, NRCS, 2014). Non-native taxa were considered 'invasive' if they were included in the USDA Plants 'Weedy and Invasive Plants' lists for major eastern US regions. Non-natives whose native distributions included any region in the contiguous USA were not included, thereby preventing analysis of non-native taxa that originated from the western USA

(see Fridley (2008) for further information and the full ENA dataset). We compared this species list with the invasive list of The Invasive Plant Atlas of the United States (US NPS & University of Georgia CISEH, 2016). After accounting for native species and those reported outside ENA, there were only 12 species that were not also listed in Fridley (2008), of which most were either not considered due to unclear native or unclear invasion status in ENA (few known occurrences). Therefore, we used Fridley (2008) in the present analysis for ENA.

EAS naturalized flora

We assembled a dataset for the naturalized and invasive vascular plant taxa in EAS from various sources (Table S1). Published and unpublished regional lists were compiled for China (Weber *et al.*, 2008; Jiang *et al.*, 2011; Axmacher & Sang, 2013), South Korea (Korea Forest Service, 2016), North Korea (Pak *et al.*, 2009) and the Russian Far East (Kozhevnikov & Kozhevnikova, 2011). Our dataset includes all major EAS regions except Japan (due to lack of available data) (see metadata in Appendix S1 for a complete list of data sources).

Floristic region native range data

The native range of each species was assigned to one or more of the global floristic regions of Takhtajan (1986). This scheme defines phytogeographical regions based on areas of endemism and major centres of plant diversification (see Fridley, 2008) and ignores political boundaries. Native species ranges were assigned primarily through information from the USDA Germplasm Resources Information Network (USDA, ARS, National Genetic Resources Program, 2010). Following Fridley (2008), three regions in Australia were merged, as were three small South African regions due to small sample sizes and accuracy of distribution data. Fifty taxa with unknown or unclear native ranges were excluded from the analysis.

Habitat classification

The habitat affinities of each invader were placed into one or more of seven categories, using the scheme of Fridley (2008;

Table 1 Habitat categories and description for plant invaders, grouped according to general descriptions in major floras, following Fridley (2008).

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 and ridgetop woods
Managed	Unshaded habitat that is the product of continuing disturbance (annual or frequent), 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 thickets, waste places, disturbed areas, old fields, sandy shores, hedgerows, fence lines, woodland edges, wood borders, fields, trails, urban lots, dunes, coastal sands and meadows
Riparian	Habitats associated with flowing water, including riparian, streamside, stream banks, river banks, gravel bars, riverine forest, bottomland, floodplains, riverine woods, rivers and floodplain forest
Roadside	Frequently disturbed habitat associated with transport, including roadsides, road banks, road ditches, right of ways and railway embankments
Wetland	Seasonally or continually wet terrestrial habitats, including wetland, seeps, ditches, bogs, marshes, lowlands and waterways

Each invasive species was assigned to one or more habitats.

Table 1). This classification uses repeated patterns in habitat descriptions from floras to standardize habitat information across regional lists, while minimizing the number of categories for analysis of general trends. Non-invasive species were not analysed by habitat due to low abundances in the introduced range (by definition); habitat affinities in the introduced range are typically not recorded or known for non-native species of low abundance. Habitat information for ENA invaders can be found in Fridley (2008). Habitats for EAS invaders were determined using descriptions in the Flora of China (eFloras, 2008), regional floras and expert opinion (Appendix S1).

Analyses

Contingency tables of floristic region provenance by habitat and by growth form were analysed for independence using chi-square tests in R (R Core Team, 2015) to determine whether regional patterns were significantly different. To further detect which outliers influenced these potential regional differences, significant residual outliers were

identified with the Freeman–Tukey deviate statistic (Sokal & Rohlf, 1995), with a threshold of an expected count of at least five for significance (Legendre & Legendre, 1998). Patterns were visualized with world maps using the ‘mapproj’ package in R (Bivand & Lewin-Koh, 2016).

RESULTS

EAS and ENA naturalized floras

EAS includes 1293 naturalized taxa, the majority of which originate from the Circumboreal (including Europe; 32%), central Asian (Irano-Turanian region; 28%) and Mediterranean (25%) regions (Table 2; note that this does not sum to unity, as taxa can be native to more than one region). EAS contains 51% fewer naturalized species (1336) overall compared with ENA (2629). Despite this difference, naturalized species in both regions are from similar native regions (corresponding ENA regional representation: Circumboreal 45%, Irano-Turanian 31% and Mediterranean 39%). In EAS, 75 non-native taxa are endemic to ENA (native to a single region; 47% invasive), compared with ENA with 291 endemic non-natives from EAS (25% invasive).

EAS and ENA invasive floras

EAS has significantly more invaders than ENA, both in terms of the absolute number of species (531 vs. 449) and as a fraction of the total naturalized flora (41% vs. 17%). However, the majority of invaders in both regions originate from temperate/Mediterranean donor regions in the Northern Hemisphere (Fig. 1), with the exception of a high contribution from the Caribbean region in EAS (Fig. 1a) but not ENA (Fig. 1b). Considering the proportion of naturalized species considered invasive, ENA invasions are overrepresented by Northern Hemisphere regions, including Saharo-Arabian (42% invasive), EAS (29%), Irano-Turanian (27%) and Circumboreal (22%) regions. Considering only regional endemics (native to a single region), the East Asian contribution remains high (25% invasive), while the invasive percentages for the other regions decline toward zero as invaders with large geographical ranges are excluded (Fridley, 2008). In contrast, temperate zone regional taxa more uniformly invade EAS (from 44% to 50% invasive; Table 2), and, unlike the pattern for ENA, tropical and Southern Hemisphere regions are important donors, including Central and South America (Caribbean, Amazonian, Brazilian, Andean, Chile-Patagonian; 43–49%) and Saharo-Arabian (51%).

Taxonomic invasion patterns

We found large differences in the taxonomic composition of ENA and EAS invaders. Although naturalized floras of both regions are dominated by Poaceae and Asteraceae (Fig. 2), the Asteraceae accounts for 21% of all invaders in EAS, compared with only 9% in ENA. Over half (54%) of all

Table 2 East Asian (EAS;China, Russian Far East, South Korea, North Korea) and eastern North American (ENA; Fridley, 2008) naturalized and invasive floras categorized by global donor floristic regions (Takhtajan, 1986).

No.	Region name	EAS				ENA				Invasive/naturalized (region endemic)			
		Naturalized taxa	Invasive taxa	Invasive/naturalized	Invasive/naturalized	Naturalized taxa	Invasive taxa	Invasive/naturalized	Invasive/naturalized				
1	Circumboreal	414 (0.32)	197 (0.37)	0.48	73 (0.19)	32 (0.23)	0.44	1196 (0.45)	266 (0.59)	0.22	282 (0.3)	31 (0.25)	0.11
2	EAS	NA	NA	NA	NA	NA	NA	622 (0.24)	180 (0.4)	0.29	291 (0.31)	74 (0.6)	0.25
3	ENA	215 (0.17)	106 (0.2)	0.49	75 (0.19)	35 (0.25)	0.47	NA	NA	NA	NA	NA	NA
4	Rocky Mountains	68 (0.05)	34 (0.06)	0.50	3 (0.01)	0 (0)	0.00	NA	NA	NA	NA	NA	NA
5	Macaronesian	113 (0.09)	46 (0.09)	0.41	5 (0.01)	1 (0.01)	0.20	303 (0.12)	53 (0.12)	0.18	1 (0)	0 (0)	0.00
6	Mediterranean	328 (0.25)	147 (0.28)	0.45	18 (0.05)	6 (0.04)	0.33	1027 (0.39)	205 (0.46)	0.20	143 (0.15)	3 (0.02)	0.02
7	Saharo-Arabian	71 (0.05)	36 (0.07)	0.51	2 (0.01)	0 (0)	0.00	105 (0.04)	44 (0.1)	0.42	1 (0)	0 (0)	0.00
8	Irano-Turanian	363 (0.28)	168 (0.32)	0.46	73 (0.19)	26 (0.19)	0.36	815 (0.31)	220 (0.49)	0.27	68 (0.07)	2 (0.02)	0.03
9	Madrean	200 (0.15)	94 (0.18)	0.47	18 (0.05)	7 (0.05)	0.39	42 (0.02)	8 (0.02)	0.19	14 (0.02)	3 (0.02)	0.21
10	Guineo-Congolian	50 (0.04)	14 (0.03)	0.28	1 (0)	0 (0)	0.00	93 (0.04)	11 (0.02)	0.12	1 (0)	0 (0)	0.00
11, 13, 28	South African	39 (0.03)	10 (0.02)	0.26	3 (0.01)	1 (0.01)	0.33	92 (0.03)	8 (0.02)	0.09	6 (0.01)	0 (0)	0.00
12	Sudano-Zambesian	90 (0.07)	27 (0.05)	0.30	9 (0.02)	1 (0.01)	0.11	189 (0.07)	20 (0.04)	0.11	13 (0.01)	0 (0)	0.00
15	Madagascan	32 (0.02)	7 (0.01)	0.22	4 (0.01)	2 (0.01)	0.50	52 (0.02)	6 (0.01)	0.12	1 (0)	0 (0)	0.00
16	Indian	61 (0.05)	21 (0.04)	0.34	14 (0.04)	2 (0.01)	0.14	147 (0.06)	26 (0.06)	0.18	12 (0.01)	2 (0.02)	0.17
17	Indo-Chinese	37 (0.03)	10 (0.02)	0.27	5 (0.01)	1 (0.01)	0.20	153 (0.06)	28 (0.06)	0.18	4 (0)	2 (0.02)	0.50
18	Malasian	36 (0.03)	6 (0.01)	0.17	7 (0.02)	3 (0.02)	0.43	149 (0.06)	22 (0.05)	0.15	1 (0)	0 (0)	0.00
23	Caribbean	254 (0.2)	108 (0.2)	0.43	41 (0.11)	15 (0.11)	0.37	96 (0.04)	9 (0.02)	0.09	18 (0.02)	1 (0.01)	0.06
25	Amazonian	167 (0.13)	75 (0.14)	0.45	6 (0.02)	2 (0.01)	0.33	66 (0.03)	10 (0.02)	0.15	3 (0)	1 (0.01)	0.33
26	Brazilian	188 (0.15)	83 (0.16)	0.44	15 (0.04)	3 (0.02)	0.20	157 (0.06)	14 (0.03)	0.09	22 (0.02)	2 (0.02)	0.09
27	Andean	168 (0.13)	74 (0.14)	0.44	8 (0.02)	1 (0.01)	0.13	99 (0.04)	8 (0.02)	0.08	13 (0.01)	0 (0)	0.00
29, 30, 31	Australian	22 (0.02)	5 (0.01)	0.23	3 (0.01)	1 (0.01)	0.33	103 (0.04)	9 (0.02)	0.09	10 (0.01)	0 (0)	0.00
33	Chile-Patagonian	94 (0.07)	46 (0.09)	0.49	5 (0.01)	1 (0.01)	0.20	132 (0.05)	11 (0.02)	0.08	20 (0.02)	2 (0.02)	0.10
35	Neozeylandic	4 (0)	0 (0)	0.00	0 (0)	0 (0)	0.00	7 (0)	0 (0)	0.00	1 (0)	0 (0)	0.00
	Cultivation origin	50 (0.04)	12 (0.02)	0.24	NA	NA	NA	141 (0.05)	9 (0.02)	0.06	NA	NA	NA
	All regions	1293	531	0.41	388	140	0.36	2629	449	0.17	925	123	0.13

Region endemics refer to those taxa native to one floristic region only. Numbers in parentheses refer to the overall proportions for each region (region count/column total).

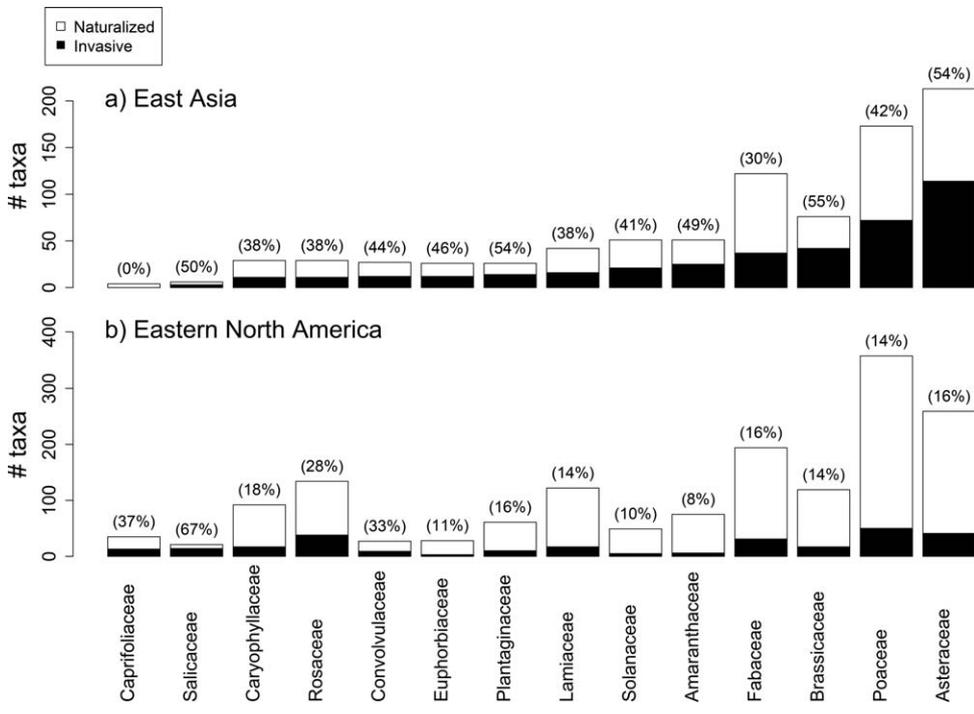


Figure 2 Naturalized and invasive taxa belonging to the top 10 families contributing the most invaders in (a) East Asia and (b) Eastern North America. Numbers in parentheses above each bar denote the percentage of naturalized taxa within each family that are invasive.

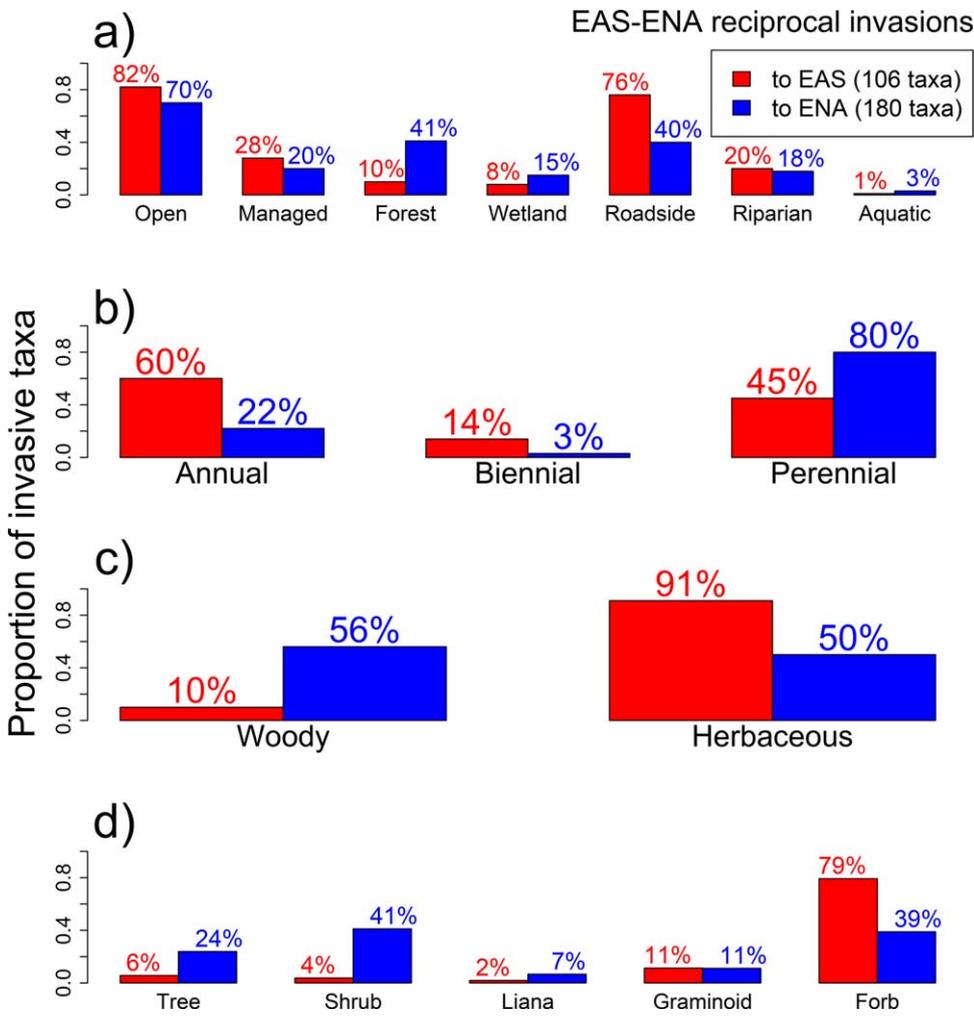


Figure 3 Invasion patterns for reciprocal invasions between Eastern North America (ENA) [black (blue online), $n = 180$] and East Asia (EAS) [white (red online), $n = 106$]. Bars show overall percentages by region according to (a) invaded habitat, (b) life duration, (c) habit, and (d) growth form. Note that some species can be described by multiple categories (does not sum to 100%).

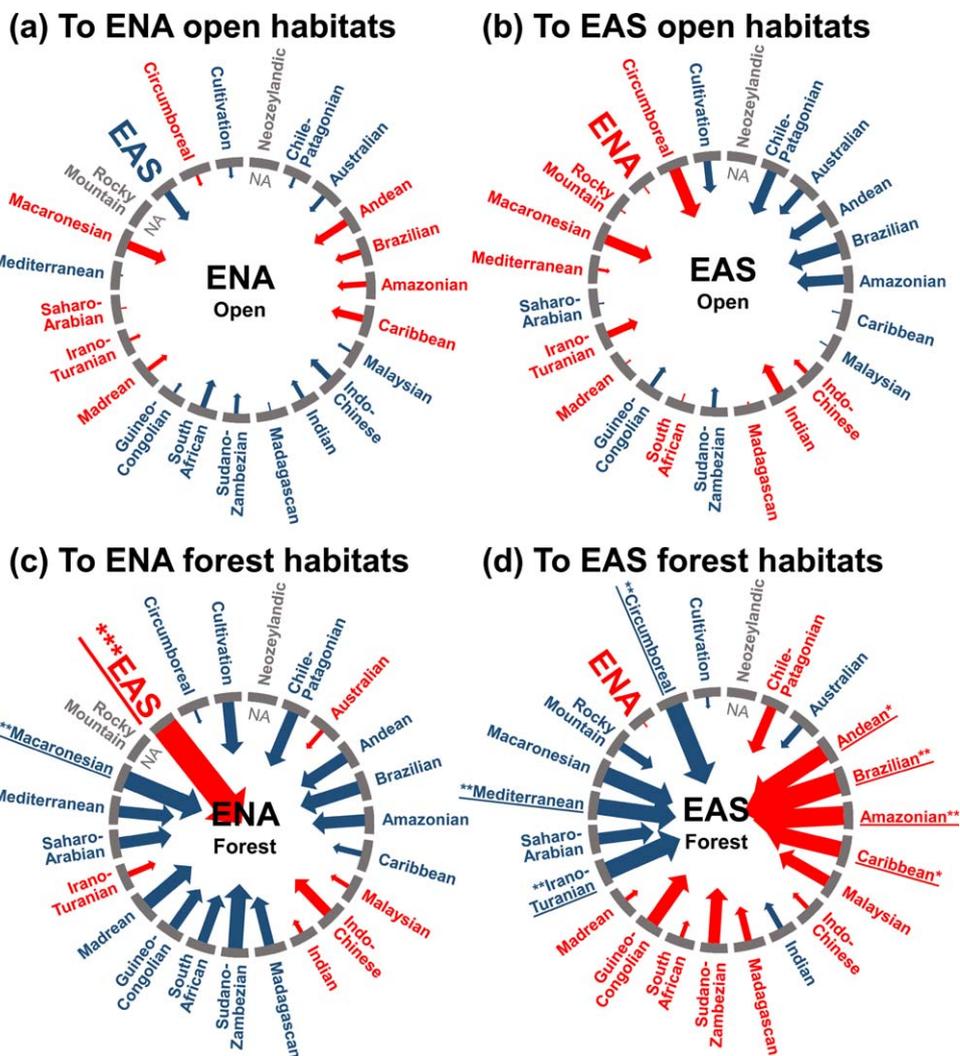


Figure 4 Biogeographical patterns of plant invasions into (a,b) open and (c,d) forest habitats in East Asia (EAS) and eastern North America (ENA). Arrow sizes are proportional to the log-transformed standardized residuals from Pearson chi-square analyses of contingency tables of all floristic region of origin and habitat types. Grey arrows (blue online) denote negative values; black arrows (red online) denote positive values. Regions that are significant outliers are underlined: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

naturalized Asteraceae in EAS are invasive, in large contrast to only 16% in ENA (Fig. 2). Asteraceae is the largest donor of ENA endemics to EAS (28 species, 57% invasive), again in contrast to only four endemic Asteraceae species from EAS to ENA (none of which are invasive). Plant families that are absent (or nearly so) in the EAS naturalized flora are among the top invaders in ENA, including, for example, Adoxaceae (11 naturalized, 45% invasive in ENA; none naturalized in EAS), Berberidaceae (7 naturalized, 57% invasive in ENA; none naturalized in EAS), Caprifoliaceae (35 naturalized, 37% invasive in ENA; only 4 naturalized, none invasive in EAS) and Sapindaceae (11 naturalized, 64% invasive in ENA; only 2 naturalized, 1 invasive in EAS). Further, Rosaceae contributes the third highest number of invaders to ENA (8% of all invaders) but accounts for only 2% of invasions in EAS (Fig. 2).

Habitat-level invasion patterns

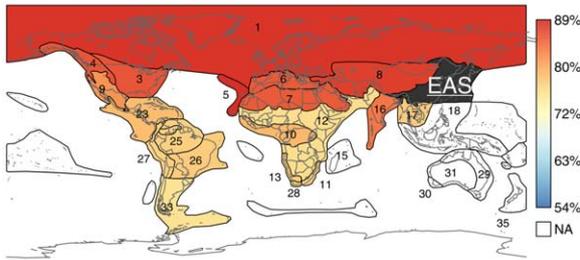
We found similarly large differences in the level of invasion of most habitat types in EAS and ENA (Appendix S2) and

contrasting geographical origins of invaders in the same habitat across regions (Appendix S3). On the one hand, a similar proportion of invaders are found in open habitats in EAS (75%) and ENA (74%), as well as managed (29% EAS, 34% ENA), riparian (15% EAS, 13% ENA) and aquatic habitats (1% EAS, 4% ENA). On the other hand, forest habitats have many fewer invaders in EAS than ENA (9% vs. 29%), as do wetland habitats (4% vs. 13%), whereas roadside habitats have more invaders in EAS (72% vs. 44%). These patterns are magnified when narrowing the comparison to reciprocal invaders between regions (Fig. 3). Almost half (41%) of invaders originating from EAS can be found in ENA forests, whereas only 10% of invaders originating from ENA are present in EAS forests.

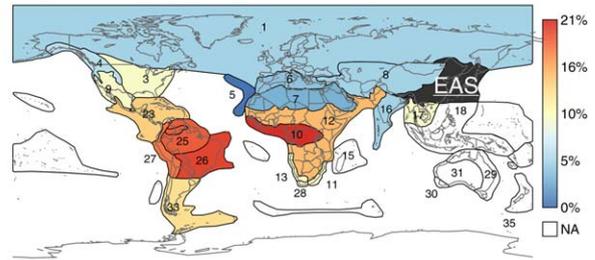
We also found strong biases in invader provenance among habitat types for both regions (EAS, overall habitat \times region $\chi^2 = 192.3$ on 126 d.f.; ENA, overall habitat \times region $\chi^2 = 243.6$ on 120 d.f.; $P < 0.001$; Appendix S3). Significantly more invaders native to EAS are found in ENA forests compared with the overall invasive pool ($P < 0.001$), but ENA taxa invade all EAS habitats in the expected

East Asian (EAS) invasions:

a) open habitats

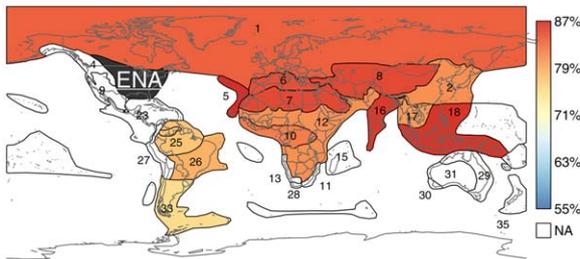


b) forest habitats



E. North American (ENA) invasions:

c) open habitats



d) forest habitats

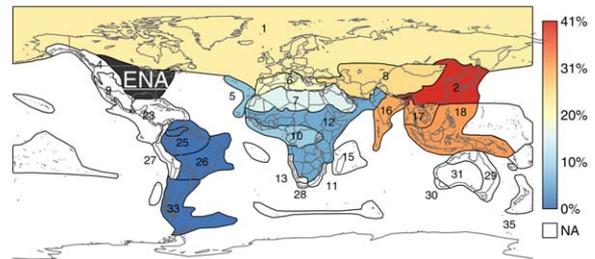


Figure 5 Proportion of naturalized species that are invasive (% invasive) from each donor region invasive in open and forest habitats in (a,b) East Asia (EAS) and (c,d) eastern North America (ENA). Data for regions in white are not plotted due to low sample sizes (<10 invaders).

proportion based on overall counts (all $P > 0.05$; Fig. 4, Appendix S3). More invaders are from the Neotropics than expected in EAS (Caribbean, $P < 0.001$; Amazonian, Brazilian, both $P < 0.01$), but not in ENA (all $P > 0.05$). Mediterranean herbs are overrepresented in managed habitats in both ENA and EAS (all $P < 0.05$), and open habitats in EAS and ENA are similarly invaded by species from north temperate regions (Fig. 5a,c). This is in strong contrast to forest invasion patterns (Fig. 5b,d), where woody ENA invaders from EAS are overrepresented ($P < 0.001$; Table 2) compared with few woody invaders in EAS (14%; compared with 39% in ENA).

Shared naturalizations between regions

In order to directly compare ENA and EAS and partially control for introduction effort, we also analysed invasion patterns for the subset of taxa that have naturalized in both regions (Appendix S4). EAS and ENA share 465 naturalized taxa, of which 81 are invasive in both regions. Similar to the overall pattern (Table 2), EAS has significantly more invaders than ENA in this shared species subset, both in terms of absolute species number (219 vs. 131) and as a fraction of the naturalized flora (47% vs. 28%). Patterns in provenance in this subset of data are similar for invasive taxa (Appendix S4). Further, the top invasive families are largely shared (Asteraceae, Brassicaceae, Poaceae) but some

families are not represented in this shared dataset (e.g. Caprifoliaceae species are only invasive in ENA). These shared taxa also show similar habitat-level invasion patterns to the full dataset (Fig. 3), with particularly high proportions of invaders found in open habitats (EAS, 80%; ENA, 85%; see Appendix S4). ENA forests are more invaded than EAS forests (15% vs. 5%), as are EAS roadsides compared with those in ENA (79% vs. 58%). Invasion biases in life-history and growth-form characteristics in the overall dataset (Fig. 3b–d) are absent, with similar invasion patterns in EAS and ENA. In particular, with the removal of the many woody species that originated in EAS—an unavoidable artefact of this particular subset of shared naturalized species—ENA is similarly invaded by woody species compared with EAS (9% vs. 10%; compared with 39% vs. 14% in the full dataset; Appendix S4).

DISCUSSION

Our analysis of the naturalized and invasive plant species pools of two climatically similar regions confirmed a strong role for origin effects (Buckley & Catford, 2016), the nature of which varied by region, habitat type and their interaction. On the one hand, open habitat types, including frequently disturbed ecosystems, are dominated by non-native European weeds (Circumboreal and Mediterranean floristic regions) in both EAS and ENA. This accounts for the

shared predominance of light-loving phylogenetic groups (Poaceae, Brassicaceae, Asteraceae, Fabaceae) as invaders across regions, and is consistent with long-held notions of the invasiveness of the European flora as a function of cultural expansion of European populations across the temperate world over the past 500 years (di Castri, 1989). Our analysis suggests that disturbed habitats throughout EAS are subject to the same ecological processes that drive such invasions world-wide, consisting of species of high colonizing ability, fast growth rates and tolerance of disturbance regimes associated with common management practices (mowing, grazing; Mack, 1989; Fridley, 2008).

On the other hand, forest habitats, which are the dominant vegetation type in undisturbed areas across each region, diverged strongly in their overall invasibility and the nature of their origin effects between EAS and ENA. This forest invasion bias was further reflected in the predominance of woody invaders in ENA and in the representation of woody families as invaders (including Adoxaceae, Berberidaceae, Caprifoliaceae; note that most Rosaceae invaders in ENA are also woody). We were particularly surprised by the overrepresentation of woody invaders from Central and South American floristic regions in EAS forests. Together with the overall low frequency of invaders in forest habitats in EAS, our analysis suggests that shade-tolerant, woody invaders are scarce in the EAS temperate zone, but that New World woody invaders increase in subtropical forests and woodlands, such as those in southern China (Weber *et al.* 2008). It is notable that forests of the south-eastern USA also have a significant pool of woody invaders, but generally of Old World provenance (Fridley, 2008). Previous studies have well documented the many ecological, historical and phylogenetic relationships between EAS and ENA floras (e.g. Boufford & Spongberg, 1983; Guo *et al.*, 1998; Guo, 1999; Qian & Ricklefs, 1999; Wen, 1999) but few studies have compared plant naturalizations across these regions. Guo *et al.* (2006) compared range sizes of a subset of native and non-native plants in EAS and ENA, finding more EAS species in ENA, and with larger distributions than vice versa. We confirm that this imbalance is present at the invasive level: EAS species account for 40% of all invaders in ENA, but in EAS only 20% of invasive species have native distributions in ENA.

We were also surprised to discover a large imbalance in the growth form of invaders exchanged between EAS and ENA: of those species with native ranges restricted to either region, those from EAS that invade ENA are mostly woody (56%; 86% considering endemics only), while ENA species invasive in EAS were mostly herbaceous (91%; 86% for endemics). This pattern is striking given the predominance of forest vegetation across both regions—why would ENA herbaceous species be unusually invasive in EAS? Using a more limited dataset, Fridley (2013) hypothesized that the bias in invader growth forms is due in part to the contrasting evolutionary histories of EAS and ENA. EAS and ENA currently share similar climate and soil conditions (Guo,

1999), with mesophytic forest communities that were colonized by similar lineages throughout much of the Tertiary (Donoghue & Smith, 2004). During the mid-Tertiary and particularly during the Miocene, ENA and EAS shared strong floristic connections, and recent phylogenetic studies have shown that many temperate forest clades originated and diversified in EAS (Donoghue & Smith, 2004), with many ENA species tracing their ancestry back to EAS. Estimates of climatic conditions since the end of the Miocene (*c.* 5 Ma), however, suggest repeated and extensive episodes of extreme cold in relatively low latitudes in ENA that were generally absent in EAS, which may have facilitated the persistence of open habitats in ENA even up to the Holocene (Marks, 1983; Adams & Faure, 1997; Salzmann *et al.*, 2011). Given that the putative historical frequency of open habitats corresponds well with the taxonomic diversity of mesic, open-habitat herbs in ENA compared with the rest of the Northern Hemisphere (particularly Asteraceae), and that many of these herbs are invasive throughout meadow habitats in the temperate world (Fridley, 2013), it is at least suggestive that evolutionary mechanisms relating to pre-adaptation are driving the biogeographical invasion patterns reported here. That is, the geological-scale predominance of closed forest habitats in EAS, and the more recent historical abundance of meadow habitat in ENA, has allowed natural selection to produce more competitive lineages of plants in these respective habitats and regions today (Fridley & Sax, 2014). We caution that this is only a hypothesis, and one that needs much more investigation at the physiological level (Heberling & Fridley, 2012, 2013).

It is important to consider the alternative explanation that the invasion patterns we describe between EAS and ENA are largely the result of human activities or cultural bias. First, introduction effort, both accidental and intentional, likely differs between EAS and ENA, especially when considering the history of European exploration and traditions of plant collecting and cultivation (Boufford, 2001). In fact, many non-native horticultural species currently grown in ENA originated in EAS (Olsen, 2013). However, it is unlikely that introduction effort alone dictated the patterns we report. We partially controlled for introduction effort by analysing invasions as a proportion of the total naturalized pool (% invasive), rather than only considering the absolute number of invaders (Richardson & Pyšek, 2012). Second, the definition of ‘invasive’ is notoriously difficult to standardize across political regions (Pyšek *et al.*, 2004). EAS has 51% fewer naturalizations than ENA, yet a substantially larger proportion of the naturalized flora we document as invasive (41% vs. 17%). However, it is clear that the ‘tens rule,’ which predicts that 10% of all naturalized taxa are also invasive (Williamson & Fitter, 1996), does not hold for ENA (17%) or EAS (41%). One reason for the discrepancy in invasion proportions could be differences between regional sources in their definition of ‘invasive’. Although we were careful to use the same working definition for invasive status across regions (Richardson *et al.*, 2000), it is not possible to estimate whether a

significant proportion of the difference in invasiveness across regions is due to different methods of observation in different countries. For this reason, we have chosen to highlight proportional differences in the types of habitats, native provenances, taxonomy and growth forms between regions as a measure of invasibility of a region, rather than absolute numbers of invaders.

Conclusion

In the first compilation of invasion patterns across the entire East Asian floristic region outside Japan, we found strong asymmetries in plant invasion patterns across this region and Eastern North America (ENA), with East Asia (EAS) particularly vulnerable to herbaceous invaders in open and roadside habitats, and ENA biased toward invasion into forests by woody species from EAS. It remains largely unknown whether these habitat-level patterns can be explained by differential climate or land-use histories between regions. Our results suggest that modern exchanges between EAS and ENA might be a continuation of historical colonization of EAS lineages into ENA that involve an EAS flora specialized to an ancient and relatively stable temperate, mesic climate. Given the strong directionality in invasion patterns, our results strongly support the importance of 'origin effects' in plant invasions. As plant communities continue to be reshuffled through human introduction, we expect large differences in the invasibility of particular regions and habitats as a consequence of their contrasting evolutionary histories.

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DATA AVAILABILITY STATEMENT

The complete EAS dataset is available in Appendix S1. The ENA dataset is publicly available in Supporting Information in Fridley (2008).

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SUPPORTING INFORMATION

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

Appendix S1 Naturalized and invasive taxa in East Asia and associated metadata.

Appendix S2 Comparisons by habitat and growth form for all invasions.

Appendix S3 Results from Pearson chi-square analyses on habitat by region of origin for invaders in East Asia and eastern North America.

Appendix S4 Results from subset analysis on shared naturalized taxa between regions.

BIOSKETCH

This project originated in 2013 at the Fridley Lab at Syracuse University. **J. M. Heberling** (currently a post-doc at the University of Tennessee) and **I. Jo** (currently a post-doc at Purdue University) were PhD students in the Fridley Lab. We sought to understand whether biogeographical biases in eastern US plant invasions were similar to those elsewhere. **J. D. Fridley** motivated the study and analysed ENA data. **I. Jo** and **H. Lee** constructed the Korean database and **A. Kozhevnikov** assembled data for the Russian Far East. **J. M. Heberling** coordinated the project and led the analysis and writing.

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