

Lengths and correlates of lag phases in upper-Midwest plant invasions

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Abstract There are often *lag phases* in plant invasions, seemingly dormant periods between arrival in a new range and rapid population growth. Lags impede prioritization of invasive-species control efforts: when eradication is most feasible, it is often unclear whether a species is benign or a potentially harmful “sleeper weed.” I used herbarium records to estimate lag phases for invasive or potentially invasive plant species in three regions of the upper Midwest. I tested whether factors related to species’ invasion epidemiology, traits, or the habitats they invade were correlated with lag lengths. From an initial pool of 151 species, there were sufficient records to test for lags in 76 for northern Wisconsin, 90 for southern Wisconsin, and 91 for the southern Lake Michigan region. Lags were identified in 77% (197) of these 257 datasets and ranged from 3–140 years with a mean of 47.3 ± 34.6 (SD). Lags differed by native range, introduction pathway, growth form and habit, dispersal mode, flowering phenology, pollination mode for a subset of species, and breadth, light availability, and water availability of invaded habitats. However, estimated lags were highly variable and tested factors did not

have strong explanatory power. Exotic species comprised an increasing proportion of total herbarium records. Of the species with known introduction pathways, 85% were intentionally introduced, mainly as ornamentals. The long durations, high variability, and low predictability of lags, along with human culpability for an increasingly non-native flora, support a cautious approach to species introductions.

Keywords Exotic species · Herbarium data · Lag phase · Logistic growth · Species traits · Von Bertalanffy growth function

‘A vile weed.’ (*Rumex acetosella*, 1861).

‘A very bad weed.’ (*Salsola tragus*, 1937).

‘...this horrendous weed grows in solid stands by the 1000s...’ (*Alliaria petiolata*, 1997).

—Comments by collectors of Wisconsin herbarium specimens.

Introduction

Only a small proportion of introduced plant species become the *invasive* species that cause great ecological and economic harm (Pimentel et al. 2005; Vitousek et al. 1997; Williamson and Fitter 1996). Unfortunately, it is very difficult to target the species most likely to become invasive from a candidate pool that may be much larger (Daehler 2003; Moffitt and Osteen 2006).

One impediment to prioritization is that invasion is a complex, multi-stage process. Nonindigenous species

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have to overcome numerous hurdles to transition from a new colonist to a problematic invader: survive transport, persist after arrival, reproduce, have descendants persist and reproduce, become naturalized, and become widespread/dominant (Colautti and MacIsaac 2004; Mack et al. 2000). Successful invaders beat long odds through a confluence of their traits with a hospitable environment, human facilitation, and sometimes evolutionary or trophic mechanisms (Callaway and Ridenour 2004; Daehler 2003; Ellstrand and Schierenbeck 2000; Mack et al. 2000; Zedler and Kercher 2004). Some exotic species have been given many opportunities to become invasive through widespread sale, transport, and cultivation, yet have not done so (e.g., ornamentals like *Forsythia*, *Hosta*, lilac, and peony species in the temperate US). Other species were not intentionally introduced or receive little *deliberate* human assistance but have traits that enable them to spread aggressively, such as *Euphorbia esula* (leafy spurge), *Potamogeton crispus* (curly-leaf pondweed), and *Pastinaca sativa* (wild parsnip).

A characteristic pattern associated with species overcoming obstacles on the path to invasiveness is the *lag phase*: a period of slow population growth between introduction or establishment in a new range and inflection to more-rapid population growth, which may then taper off as the species saturates its new range (Mack et al. 2000). These periods of relative dormancy may be a consequence of time needed to overcome demographic constraints or the Allee effect; for genetic structure to change as rare, pre-adapted genotypes or newly emerging genotypes are selected for, to reach a threshold of dispersal across the landscape from which invasion can quicken; or for environmental or biotic conditions to change beneficially for the new species (Crooks 2005; Mack et al. 2000). Lags can last for decades, making it unclear whether a given species is unlikely to become invasive or is a “sleeper weed” (sensu Cunningham et al. 2003) that could cause problems in the future.

Lag phases are not often documented or quantified. They can be apparent in hindsight but rarely attract attention while underway since the relevant populations are few, small, and/or unrecognized as threats (Mack et al. 2000). Our understanding of lags is shaped largely by anecdotal observations and relatively few well-documented, sometimes spectacular examples of severe impacts following long dormancies (Crooks 2005; Mack et al. 2000). The cryptic

nature of lags leads to an unfortunate paradox: the best opportunity to control an invader comes when we are least able to recognize the threat (Crooks 2005).

Better knowledge of lag phases could inform efforts to assess the risks posed by potential invaders. For example, addition of a given species to a *white list* (designating species not deemed an invasion threat, Simberloff 2006) could be done more confidently if the species had not caused harm in a region despite being well beyond its lag phase. Conversely, species already having negative impacts at early stages should be prioritized for exclusion and control. These decisions could be facilitated if there were traits that reliably predicted lag lengths. For example, if a long-lived tree dependent on animal mutualisms for reproduction and dispersal were expected to have a longer lag phase than an annual grass, it could be subjected to a longer “probationary period.” More broadly, invasion research may be inadequately addressing naturalization and pre-impact stages of invasion (Pyšek et al. 2008). Failure to consider lags can lead to underestimation of risk in assessments of exotic species (Simberloff 2011).

Herbarium collections represent vast sources of species-occurrence data and have been used to estimate lag lengths (e.g., Aikio et al. 2010; Fuentes et al. 2008; Mihulka and Pyšek 2001). Collection data are not a substitute for thorough population studies, are constrained by variability in sampling intensity, and only approximate species’ actual abundances or distributions (Mihulka and Pyšek 2001; Pyšek and Hulme 2005). However, herbaria comprise exceptionally large datasets over broad geographic areas, often going back centuries. While differences in sampling and collection bias can be confounding, in general, species occurring more across a landscape can be expected to account for higher proportions of records.

I used Aikio et al.’s (2010) improved approach for calculating lag phases from herbarium records. This method corrects for differences in sampling intensity over time and better differentiates actual lag phases from false appearances of a lag due to data artifacts. I calculated lag lengths for exotic plant species considered invasive or potentially invasive in part of the upper Midwest (Wisconsin and the southern Lake Michigan region). I then tested whether factors related to the invasion epidemiology, functional traits, or invaded habitats of the focal species could be used to predict lag lengths. I expected lags to be shorter in

species that were native to Europe and Asia (climate compatibility and history of horticultural use), had been intentionally introduced (human facilitation) or more recently introduced (into a more anthropogenically altered landscape), were shorter-lived and herbaceous (shorter generation times), could spread clonally (not dependent on sexual reproduction), reproduced and/or dispersed abiotically (not dependent on animal mutualisms), flowered earlier and for longer periods (reproductive advantages), and invaded a diverse array of habitats and resource gradients (broad environmental tolerances).

Methods

Geographic area

I estimated lag phases for three contiguous regions defined by ecological and political boundaries. Northern and southern Wisconsin (NW, SW) are those counties mostly or entirely north or south of Curtis' vegetation *tension zone* (1959). Southern Lake Michigan (SLM) includes non-Wisconsin counties in the greater Chicago region (defined by the consortium Chicago Wilderness), encompassing parts of north-eastern Illinois, northwestern Indiana, and southwestern Michigan. The three regions include the western Great Lakes forests, upper Midwest forest/savanna transition zone, southern Great Lakes forests, and central forest/grassland ecoregions (Ricketts et al. 1999).

Focal species

I included non-native plant species that have been deemed invasive or potentially invasive within the study regions. Sources used to select species were invasive plant lists from the Chicago Botanic Garden, the City of Chicago, the Invasive Plants Association of Wisconsin, and the New Invaders Watch List (CBG 2010; City of Chicago 2009; IPAW 2003; NIWL 2010) and consultation with regional experts. This process identified 151 species.

Information was compiled from the literature and online databases for each species, including aspects of their invasion epidemiology such as native range, arrival period, and introduction pathway; functional traits like growth form and habit, lifespan, ability to

spread vegetatively, pollination and dispersal modes, and flowering phenology; and characteristics of the habitats they invade, including their diversity, association with anthropogenic disturbance, and light and water availability.

Herbarium data

For each focal species, in summer 2010 I downloaded collection records for the NW and SW regions from Wisflora and for the SLM region from vPlants (vPlants 2010; Wisflora 2010). I excluded post-2008 records to account for delays between collection and database entry. I also removed Wisflora records for plants that may have been cultivated as per collector comments. Cultivated specimens are not included in vPlants (A. Hipp, personal communication).

Interannual differences in sampling intensity or attitudes toward collecting exotic species would confound interpretations based on raw annual records. I used the approach of Aikio et al. (2010): detrending accumulation data by dividing annual records per focal species per region by the total annual records for all exotic species for each herbarium system. I also examined herbarium records for evidence of temporal changes in exotic species as a proportion of collections.

Of the initial pool of 151 species, there were 24 with no records. Of the remaining 127 species (see Online Resource 1 for full names and trait information), there were sufficient records for modeling lag phases (≥ 15 records, Aikio et al. 2010) in 91 species for SLM, 90 species for SW, and 76 species for NW. A total of 8,245 annual records representing 19,679 specimens were available for these 257 species-by-region datasets.

Lag-phase estimation

I used the method of Aikio et al. (2010) to estimate lag phases through piecewise regression modeling explicitly defining lag and increase phases. The principle is that records accumulate linearly over time during a lag phase. Species that become invasive reach an inflection point, after which gradual accumulation is replaced by accelerated, non-linear increase. The result is a two-piece model with a linear lag and a non-linear increase phase.

See Aikio et al. (2010) for detailed methods and validation. Briefly, for each species in each region, I

determined the length of a putative lag phase (t_{lag}) using an iterative, stepwise regression process. The lag phase was modeled linearly. The increase phase was modeled separately using logistic and von Bertalanffy growth (vB) functions (von Bertalanffy 1938). The chosen t_{lag} for each non-linear function was that which minimized the sum of least-squares errors for both phases. I contrasted models with and without increase phases for goodness of fit (logistic vs. vB vs. a one-piece, linear model). The best-fitting model was chosen using Akaike weights calculated from AICc values (Burnham and Anderson 2002). An additional requirement for selection of a two-piece model was that accumulation rate increase at the beginning of the non-linear phase.

A confounding factor was that earlier-arriving species had longer potential lags. For example, the baby's breaths *Gypsophila muralis* and *G. paniculata* were first collected in NW in 1903 and 1960, respectively. The longest possible lag phase for the latter was thus 57 years shorter. Data being more truncated could spuriously make it appear that lags are shortening over time. Also, lag-phase estimates showing high plasticity to years of available data would be of questionable reliability. To address this, I repeated the modeling process on a subset of data for which all species had equivalent values of t_{max} : only species with first records prior to 1958 and only the first 50 years of data for each. I contrasted results of this analysis with those from the full dataset.

Modeling was performed in R 2.10.1 (R Development Core Team 2009).

Statistical analyses

In addition to data being temporally truncated, variance of lag estimates was not constant over time. To account for these issues, I analyzed lag results using survival, i.e., time-to-event, analysis, with year of first collection as the start time, inflection year as the event time, and non-inflected datasets treated as "right-censored" (potential future inflections are unobservable) (Miller 1997). I tested potential explanatory variables with regression of a parametric survival model based on an extreme-value distribution and the data stratified by region.

Regression trees were constructed to test for interactions among variables. Regression-tree analysis

is a non-parametric method that produces a tree-like classification by recursively splitting data into increasingly homogeneous groups. Splits are evaluated based on heterogeneity between resultant groups using a log-likelihood estimate of deviance. This method is robust against correlation of variables, outliers, and non-normality (Urban 2002). Factors of little explanatory power are excluded from trees. Branches higher in a tree explain more separation and longer branches indicate greater differences between groups. The resulting tree was pruned (branches and terminal groups removed) based on a cost-complexity parameter (cp) (Venables and Ripley 2002).

Survival and regression tree analyses were performed in R 2.10.1 using the survival and rpart packages, respectively (R Development Core Team 2009; Therneau and Lumley 2009; Therneau and Atkinson 2010).

Results

Herbarium records

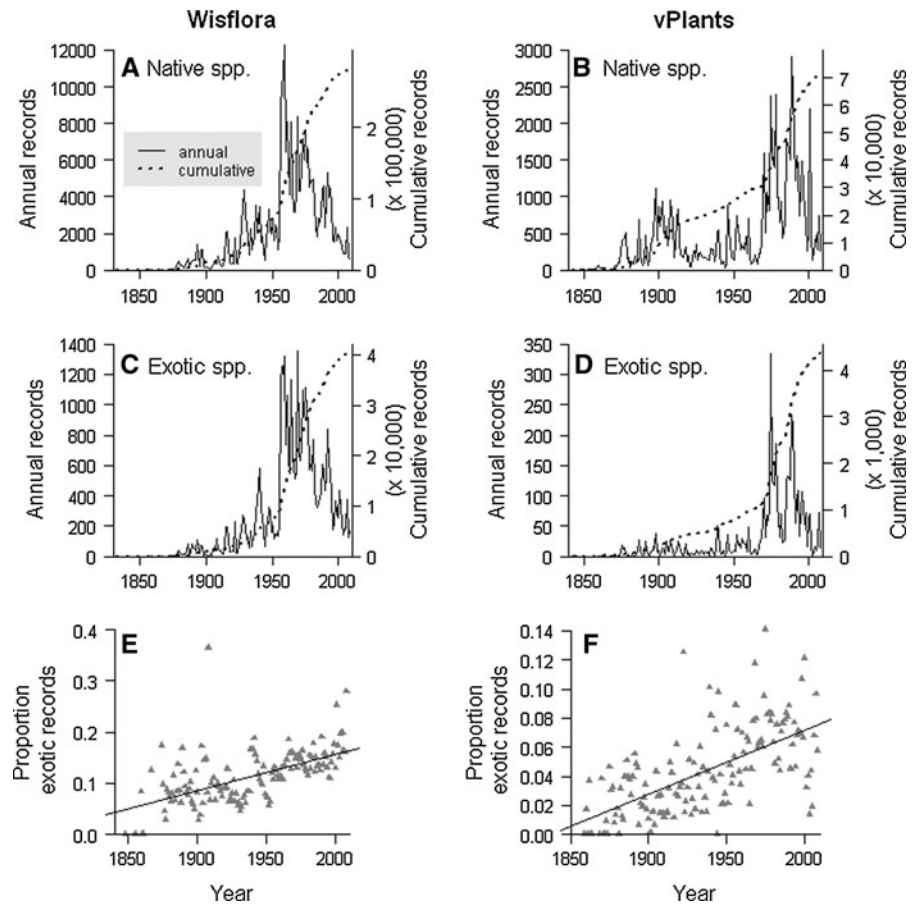
There was high interannual variability in herbarium records (Fig. 1). Cumulative records for native and exotic species followed similar patterns. Exotic records as a proportion of total records significantly increased over time for both herbaria.

Lag phases

Of the 257 species-by-region datasets with sufficient records for analysis, 197 resulted in lag-phase estimates, i.e., two-piece models with linear record accumulation followed by inflection to non-linear accumulation at an increased rate. In 46 cases, a two-piece model was selected but the rate of record accumulation did not increase in the non-linear phase. The best fit was provided by a one-piece linear model in 14 cases.

For the 197 cases exhibiting lag behavior, lag-phase range was 3–140 years, with a mean of 47.3 ± 34.6 (SD). The logistic function generally fit increase phases better than the vB function (83% vs. 17% of cases). See Fig. 2 for examples of fitted models and Fig. 3 for a summary of results. Complete lag data are available in Online Resource 2.

Fig. 1 The annual and cumulative collection records for all plant species for **a** Wisflora and **b** vPlants and for exotic species only for **c** Wisflora and **d** vPlants. Exotic species as a proportion of total records for **e** Wisflora ($P < 0.0001$, $R^2 = 0.33$) and **f** vPlants ($P < 0.0001$, $R^2 = 0.40$) (excluding years with fewer than 10 total records)



Correlates of lag lengths

Several factors were significantly or marginally correlated with lag lengths (Table 1). Lags differed by native range and introduction pathway and were shortest for species from Asia and those that arrived as contaminants. Significant species traits were growth form, with woody species having shorter lags; dispersal mode, with lags shortest in biotically dispersed species; and bloom start and duration, with lags shorter in later and more briefly blooming species. In terms of recipient habitats, species invading low-light habitats had shorter lags and there were marginal differences by habitat breadth (lags shorter for specialist species), water availability (lags shorter for aquatic invaders), and wetland-indicator status (lags shorter for wetland-dependent species).

Species with earlier first records appeared to have longer lags (Table 1, Fig. 3). However, this was an artifact of potential lag lengths of earlier-arriving species being less restricted. The truncated-data test

showed no significant relationship between first-collection year and lag length ($P = 0.60$). There was also low plasticity of the estimation method to data truncation. In 43% of cases, a dataset that had resulted in a lag failed to fit a two-piece model when restricted. For an additional 8%, a two-piece model switched to an entirely linear model. Lags estimated from truncated data did not significantly differ from estimates based on the respective full datasets (two-sample t test: $P = 0.20$).

The regression tree identified several interacting factors that influenced lag lengths but did not have high explanatory power (Fig. 4). In order of decreasing importance, significant variables were growth habit, breadth of invaded habitats, dispersal mode, and pollination mode.

Discussion

Analysis of herbarium data revealed lag phases in most of the exotic plant species evaluated. Lag phases

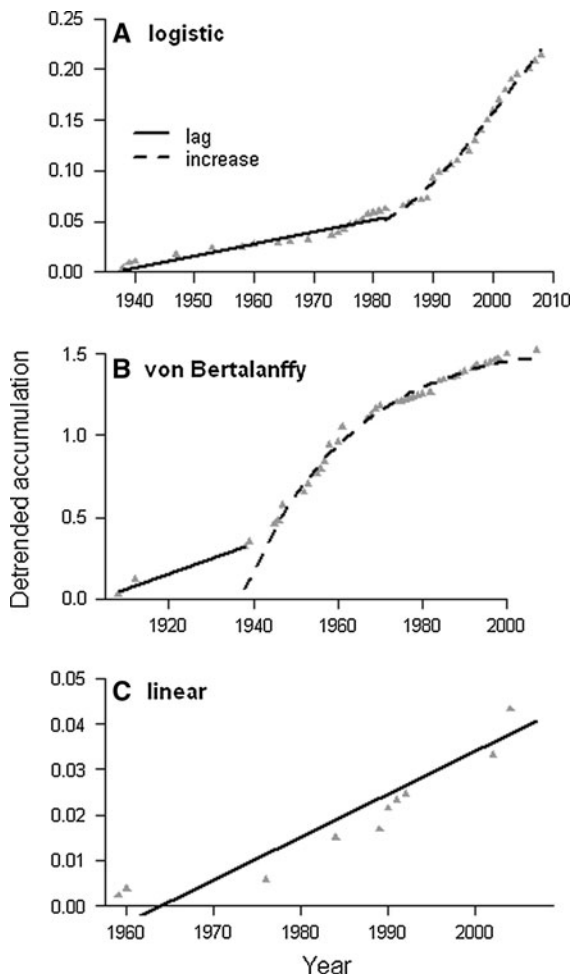


Fig. 2 Examples of model fits for two-piece models with **a** logistic and **b** von Bertalanffy increase phases and **c** a one-piece, linear model lacking inflection to a non-linear increase phase. **a** *Alliaria petiolata* in southern Wisconsin. **b** *Frangula alnus* in southern Lake Michigan. **c** *Leymus arenarius* in northern Wisconsin

averaged nearly five-decades. Factors related to invasion epidemiology, plant traits, and invaded habitats were significantly correlated with lag lengths, but often not in the manner I expected. Variability in estimated lags was high and the tested factors had only modest explanatory power.

A caveat is that lags estimated in this way are conservative as they do not account for a probable lag *before* the lag—the time between arrival of a species and it first being collected. For example, the NW lag for *Ulmus pumila* (Siberian elm) was only 7 years. It is improbable that a long-lived tree species would naturalize and become invasive over such a short

period. The calculated values of t_{lag} are minimum values that represent the observed portion of a potentially much longer biological lag.

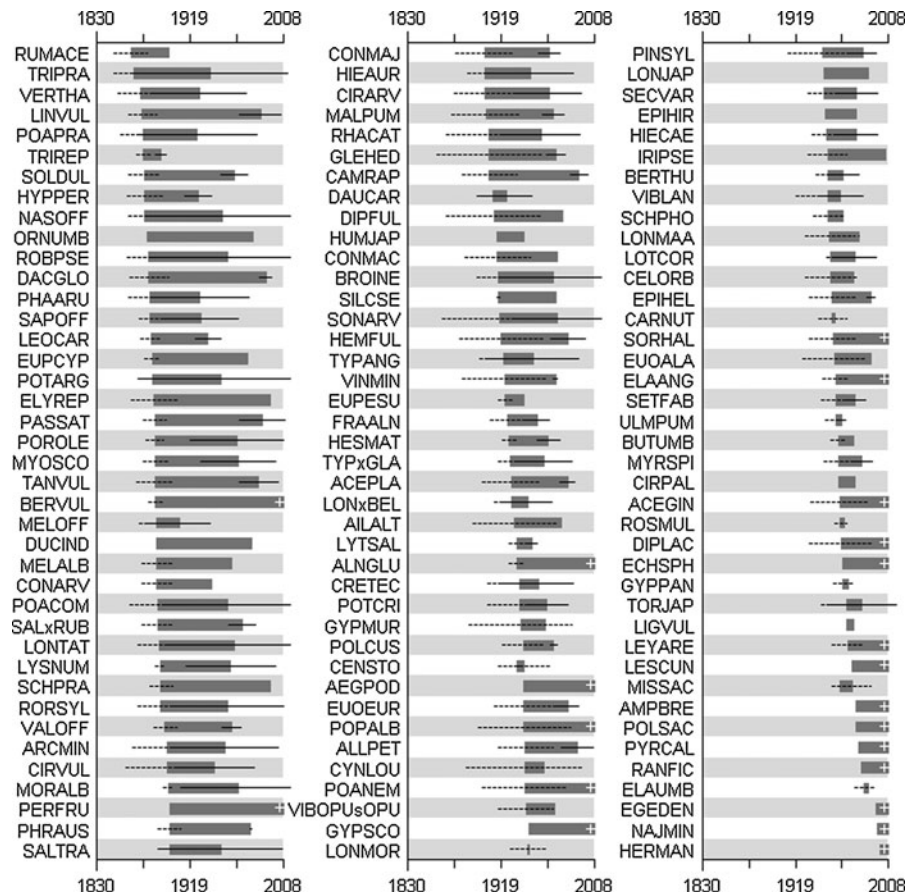
Lags were substantially shorter in species native to Asia. This may be due to high climate similarity between the study regions and parts of Asia (Widrechner and Iles 2002; Widrechner et al. 2009), including portions of northeast Asia that have high endemic plant diversity and are the origins of many horticulturally important species (Dirr 2009; Widrechner and Iles 2002). In contrast, lags were longest in the “other” native-range category, which included species native to regions of quite different climate, e.g., Africa and Europe, *Iris pseudacorus* (yellow iris) or the southern US, *Robinia pseudoacacia* (black locust).

Another significant epidemiological factor was introduction pathway. I expected intentionally introduced species to have the shortest lags due to human facilitation. However, lags were shortest in species unintentionally introduced as contaminants of ballast, crop seed, or other goods. This is likely due to contaminant species having “weedy” traits like high fecundity and dispersal rates or ability to germinate and survive under disturbed or stressful conditions (Daehler 2003).

Lag lengths were related to species’ growth forms and habits, but not as I anticipated. I thought that shorter-lived, herbaceous species would have briefer lags due to faster generation times and more rapid spread. However, lags were shorter in woody species than herbaceous species and did not differ by lifespan. In particular, they were shortest in shrubs and vines, while mean lag lengths of trees and graminoids were nearly identical.

The short lags in woody species could be due to several factors. The focal shrub species have been widely planted as ornamentals, human assistance likely to hasten spontaneous growth in natural systems (Reichard and White 2001), though the mean lag for ornamental species as a whole was <2-years shorter than the overall mean. Also, fruits of these species are often consumed by birds and other animals, facilitating seed dispersal (Bartuszevige and Gorchov 2006; McCay et al. 2009). In addition, many of the habitats in the study region (e.g., prairies, savannas, and woodlands) did not historically have well-developed shrub layers (Curtis 1959). With fire suppression in the Midwest, the landscape became more amenable to

Fig. 3 Lag-phase lengths estimated from herbarium records for 120 species ordered from earliest to latest first record. Bars span from year of first record (mean across regions) to mean inflection year (year of first record + lag length), except where *plus symbol* indicates a species that had not passed into an increase phase. Error bars are ± 1 SD for first record (*dashed*) and inflection year (*solid*) ($n = 1$ where absent). Species codes are first *three letters* of the genus and specific epithet (full names in Online Resource 1)



woody growth and canopy cover increased in many habitats (Haney and Apfelbaum 1995; Nowacki and Abrams 2008), providing suitable environments for shade-tolerant shrubs and vines like *Euonymus europaea* (European spindle-tree) and *Celastrus orbiculatus* (Oriental bittersweet). This is echoed by lags being shorter in species favoring low-light conditions (Table 1).

Lag times were shorter in species with biotic dispersal and, in a nested subset of species from the regression tree, particularly short in species with both biotic and abiotic dispersal modes. Adaptations for animal dispersal can enhance invasion ability, and dispersal mutualisms with vertebrates may primarily follow generalized syndromes not sensitive to geographic origins (Richardson et al. 2000). Thus, development of suitable dispersal mutualisms may not be limiting, allowing introduced species to reap the benefits of such arrangements with little risk.

In another nested subset of the regression tree, lags were much shorter in those species not dependent

upon animal mutualisms for pollination. This is consistent with the finding of Wiegmann and Waller (2006) that “winner” species during 50 years of plant-community change in northern Wisconsin (24% of which were exotic) were predominantly abiotically pollinated. It has been posited that invasiveness is increased by self-compatibility and unspecialized pollination syndromes (Baker 1974) but empirical results have been mixed (Richardson et al. 2000). In a phylogenetically controlled study, Burns et al. (2011) found that introduced species were more likely than native species to be self-compatible but less likely to reproduce asexually and, for introduced plants that were not self-compatible, pollen limitation was higher.

Lags were shorter in species that bloomed early (March–April) or late (July–September) in the growing season. This fits the suggestion of Crawley et al. (1996) that species occupying ends of niche axes may be able to invade more readily. Time of flowering has been identified as a significant factor in invasions of

Table 1 Summary data and results of survival analysis for potential predictors of lag lengths

Factors	Groups	Survival model			Length of lag phase			
		<i>df</i>	χ^2	<i>P</i>	Mean	SD	<i>n</i> _{lag}	<i>n</i> _{total}
<i>Epidemiology</i>								
Native range	Europe	4	22.32	0.0002	45.4	33.5	54	75
	Asia				36.2	31.9	27	31
	Eurasia				50.7	35.5	93	116
	Other				55.6	39.0	9	14
	Global				48.8	34.1	14	21
Arrival period*	Early (1844–1898)	2	273.31	<0.0001	67.1	38.8	77	111
	Mid (1899–1953)				40.6	24.7	32	106
	Late (1954–2008)				16.1	10.0	88	40
Introduction pathway	Consumption	5	17.55	0.004	56.4	35.4	19	21
	Contamination				42.9	31.9	33	45
	Cover crop				54.1	39.8	30	42
	Ornamental				45.6	32.8	86	108
	Other				44.9	38.4	15	20
	Unknown				44.6	36.4	14	21
	<i>Species traits</i>							
Growth form	Herbaceous	1	4.3	0.038	49.4	35.3	146	193
	Woody				41.6	32.1	51	64
Growth habit	Forb	4	5.24	0.26	48.8	35.3	123	157
	Graminoid				55.1	38.1	20	31
	Shrub				31.5	26.7	28	33
	Tree				56.4	35.4	18	24
	Vine				41.4	24.9	8	12
Lifespan	Annual	2	1.25	0.53	37.7	31.0	15	21
	Biennial				50.6	40.1	25	32
	Perennial				47.7	34.0	157	204
Clonal growth	No/not reported	1	0.08	0.77	48.4	36.4	64	80
	Yes				46.8	33.8	133	177
Pollination mode	Abiotic	2	0.55	0.76	43.9	35.1	44	63
	Biotic				48.8	34.4	143	177
	Both				41.6	37.1	10	17
Dispersal mode	Abiotic	3	8.82	0.032	51.3	36.6	72	94
	Biotic				40.7	33.0	46	57
	Both				47.8	35.3	65	87
	Unassisted/unknown				46.4	24.1	14	19
Bloom start	Early spring	2	10.02	0.007	42.1	33.6	35	51
	Late spring				51.0	35.1	123	158
	Summer				40.6	33.2	39	48
Bloom duration	Short (<8 weeks)	3	27.85	<0.0001	43.3	32.9	75	95
	Moderate (8–19)				48.5	34.5	77	99
	Long (19–30)				54.1	39.4	35	51
	Unknown				44.7	31.1	10	12

Table 1 continued

Factors	Groups	Survival model			Length of lag phase			
		<i>df</i>	χ^2	<i>P</i>	Mean	SD	<i>n</i> _{lag}	<i>n</i> _{total}
<i>Habitats invaded</i>								
Habitat breadth	Restricted	2	5.61	0.061	37.8	32.5	49	65
	Broad				49.3	34.8	121	157
	Generalist				56.0	34.8	27	35
Mostly anthropogenic	No	1	1.47	0.23	42.5	31.2	94	116
	Yes				51.8	37.0	103	141
Light availability	Low	3	11.05	0.011	43.3	26.0	9	10
	Medium				52.0	33.8	42	52
	High				46.3	36.1	97	134
	Mixed				46.2	34.1	49	61
Water availability	Dry	4	8.28	0.082	43.8	32.2	28	39
	Mesic				47.3	34.0	79	106
	Wetland/riparian				46.4	34.3	31	38
	Aquatic				30.7	31.7	9	10
	Mixed				53.0	37.4	50	64
Wetland indicator Status	Obligate	2	5.27	0.072	39.5	36.4	23	26
	Facultative				50.1	35.4	88	118
	Upland/unassigned				46.6	33.3	86	113

Significant or marginally significant *P* values ($\alpha < 0.10$) shown in **bold**

*n*_{lag} number of species \times region datasets resulting in a lag-phase estimate

* Differences an artifact of later-arriving species having shorter potential lag lengths

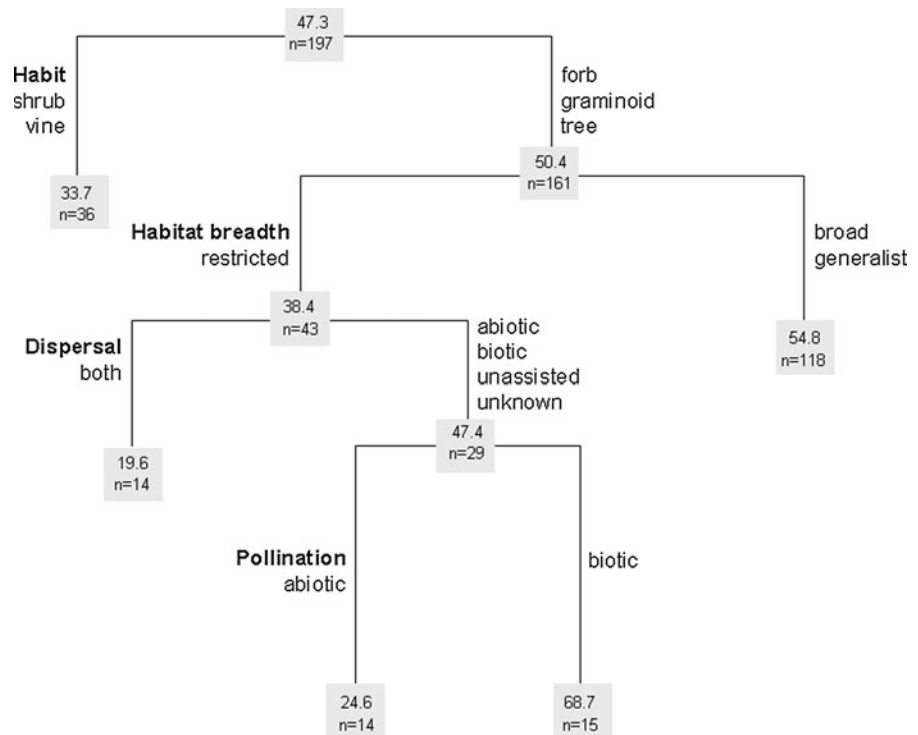
Mediterranean-climate regions (Gerlach and Rice 2003; Lloret et al. 2005), but may be less important in temperate regions (Reichard and Hamilton 1997; Thompson et al. 1995). Surprisingly, species that bloomed for shorter periods of time had shorter lags. Other studies have found longer-blooming species to be more invasive (Lloret et al. 2005; Radford and Cousens 2000). Perhaps shorter-blooming species have lower reproductive-effort costs, yielding survival, growth, or future-reproduction benefits (de Jong and Klinkhamer 2005).

A pattern that consistently emerged was habitat specialists having shorter lags than generalists. Lags were shorter for species that invade fewer habitats (by nearly two decades) or those that occupy narrow segments or ends of environmental gradients: low-light conditions, aquatic followed by dry habitats, wetland-obligate rather than facultative species. This was counter to my expectation that generalists would have shorter lags due to better dispersal ability (Dynesius and Jansson 2000). While colonization

ability may be compromised in specialists (Cadotte et al. 2006), this could be outweighed by specialists being better-adapted to exploit environmental conditions when they do reach a suitable habitat. Also, particular characteristics of certain habitats may favor invasion, such as low competition in shady environments, dispersal advantages in aquatic habitats, or high disturbance and propagule pressure in wetlands (Grime 1979; Merritt and Wohl 2002; Zedler and Kercher 2004).

There were 52 species for which lags could not be estimated (Online Resource 3). These were species that had not reached inflection to non-linear increase, had insufficient records for modeling, or lacked any herbarium records, i.e., they comprise within-lag, early-detection, and pre-detection species. Together, they form a watch list that could be used to prioritize early-detection and response efforts. Consortia such as cooperative weed management areas could use these lists for regional-scale, invasive-species management efforts. For example, within the study regions, a first

Fig. 4 Regression tree with lag lengths as the dependent variable. All factors listed in Table 1 (excluding arrival period) were included as candidate variables during tree construction. Boxes at nodes and leaves show mean lag and n for each group. Pruned tree depicted, full tree $R^2 = 0.34$



detection of *Hydrilla verticillata* (hydrilla) or early detection of *Heracleum mantegazzianum* (giant hogweed) could trigger rapid response and eradication. Longer-term efforts could be applied to eliminating or minimizing the abundance of species such as *Leymus arenarius* (lyme grass) or *Berberis vulgaris* (common barberry) that are already established but not as ubiquitous as species like *Phalaris arundinacea* (reed canarygrass) and *Rhamnus cathartica* (common buckthorn) that have long-escaped the likelihood of being controlled on all but very local scales.

The potential value of a proactive approach can be seen in hindsight. While many of the species in the present study passed the threshold to invasiveness 50–100+ years ago, others have done so recently (Online Resource 2; median inflection year: 1970, 75th percentile: 1986). There are numerous examples of invaders making the transition from regionally rare to widespread “before the eyes” of current conservation professionals. Anecdotally, this is true in the study region of species like *Dipsacus laciniatus* (cut-leaved teasel), *E. esula*, and *Phragmites australis* (common reed) (J. O’Shaughnessy, J. Steffen, E. Ulaszek; personal communication). In San Francisco Bay, *Spartina alterniflora* (smooth cordgrass) transitioned

from localized, intentional introduction in the early 1970s; through aggressive spread two decades later (Callaway and Josselyn 1992); to today, when *S. alterniflora* and its hybrids are causing great ecological harm throughout the region (Levin et al. 2006). Recent intensive efforts to eradicate invasive *Spartina* treat <1% of the infested area annually (Grijalva et al. 2008). It is impossible to know what might have happened had an aggressive response been mobilized earlier in these and other cases. However, it should generally be true that control efforts’ return on investment is inversely proportional to time since invasion.

Lag phases produce a backlog of *invasion debt* representing species already present but not yet invasive (Essl et al. 2011). Most ecosystems likely host these “sleeping weeds” (Cunningham et al. 2003), which are explicitly targeted by neither eradication nor prevention programs. The invasion debt is destined to be paid as waves of species cross the threshold into invasiveness. Unfortunately, we can only pinpoint these transitions retroactively, when the best opportunities for eradication have passed. The maturation of invasion debt is reflected in the steady increase of exotic species as a proportion of total records.

The long durations and low predictability of lags found in this study underscore the merit of a *guilty until proven innocent* or *white list* approach regarding species introductions (Mack et al. 2000; Simberloff 2006). The failure of the alternative *innocent until proven guilty* or *blacklist* strategy is illustrated by the fact that, of the 139 species in this study for which the introduction pathway is known, 85% were intentionally introduced. Of these, 72% (61% overall) were introduced for ornamental purposes. This emphasizes the particular responsibility that those in the green industry (horticulturists, landscape professionals, botanic gardens, etc.) have to be cautious in using exotic taxa and to apply stringent selection criteria (e.g., Jefferson et al. 2004).

This analysis was made possible by the rich, long-term data that herbarium collections provide and the data accessibility imparted by modern database and web tools. Insufficient investments in the size and accessibility of collections are impediments to research and conservation (Feeley and Silman 2011) at a time when novel uses of herbarium data are informing contemporary ecological questions that could not be anticipated when most herbaria were established (e.g., Robbirt et al. 2011).

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