

Spread of exotic plants in the landscape: the role of time, growth habit, and history of invasiveness

Robert G. Ahern · Douglas A. Landis ·
Anton A. Reznicek · Douglas W. Schemske

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Abstract We investigated the relative contribution of minimum residence time, growth habit, and history of invasiveness to the spread of exotic plants in Michigan and California. Our data include minimum residence time as estimated by earliest herbarium collection records, growth habit, and history of invasiveness for over 2000 records from two herbaria (MI = 943, CA = 1131). Our data support the hypothesis that minimum residence time is highly associated with landscape spread, explaining 39–44% of variation in the number of counties invaded.

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R. G. Ahern (✉)
USDA Plant Epidemiology and Risk Analysis Laboratory,
1730 Varsity Drive, Suite 300, Raleigh, NC 27606, USA
e-mail: robert.g.ahern@aphis.usda.gov

D. A. Landis
Department of Entomology, Michigan State University,
204 Center for Integrated Plant Systems, East Lansing,
MI 48824, USA

A. A. Reznicek
University of Michigan Herbarium, 3600 Varsity Drive,
Ann Arbor, MI 48108-2287, USA

D. W. Schemske
Plant Biology Department and W. K. Kellogg Biological
Station, Michigan State University, East Lansing,
MI 48824, USA

In contrast, growth habit and history of invasiveness explained a small fraction of variation in spread in California but not Michigan. Over the past 30 years exotic plant species frequently became established in Michigan and California (≥ 50 species per decade), suggesting that many more species will become invasive over time. There is an urgent need to develop effective policies for exotic plant management. In both states we found significant positive correlations between minimum residence time and species occurrence on state invasive plant lists. Further, we found historical information on the pest status of a plant species introduced into a similar environment to be relevant in determining landscape spread of exotic plants. We conclude that efforts to predict exotic species spread based on biological characteristics may have limited success, and instead endorse pest risk analysis for proposed new imports coupled with rapid detection and early response for unintended and unwanted introductions.

Keywords Environmental policy · Exotic plants · Invasion biology · Invasive species · Rates of spread · Pest risk analysis

Introduction

Ecologists have long sought to understand the factors that contribute to spread of exotic organisms (Elton

1977). However, there is no consensus regarding how introduced organisms successfully establish and spread (Hayes and Barry 2008; Kolar and Lodge 2001; Mack et al. 2000). In particular, we know relatively little about the factors that contribute to landscape spread, i.e. the dispersal of a species within a region over time (Theoharides and Dukes 2007). Biological and historical data are commonly used to assess whether a specific exotic species poses a significant risk (Pheloung et al. 1999). In the case of plants imported for propagation, these approaches typically include model-based scoring systems which classify species as likely to be invasive, not likely to be invasive, or requiring further study (Pheloung et al. 1999; Reichard and Hamilton 1997). While these approaches have been well-tested (Kolar and Lodge 2001; Reichard and Hamilton 1997), uncertainty in the assessment of invasive potential can have serious consequences. For example, carp species predicted to be innocuous in the Great Lakes (Kolar and Lodge 2002) are currently considered an important threat (Chick et al. 2003). A contrasting approach to preventing introduction of potentially invasive species is to assume that, in the absence of specific information to the contrary, all exotic species pose an unacceptable risk (Underwood 1997). If initial assessment of invasion status has an unacceptable error rate or seemingly innocuous exotics tend to become invasive over time, such precautions may be warranted.

Several groups of related hypotheses have emerged to examine establishment and landscape spread of exotic plants. Three of the most promising ideas (Heger and Trepl 2003; Rejmanek 2000) relate plant spread in new environments to: (1) residence time (Heger and Trepl 2003); (2) specific biological attributes (Goodwin et al. 1999; Reichard and Hamilton 1997); or (3) history of prior invasion success (Reichard and Hamilton 1997; Scott and Panetta 1993). While these hypotheses are not mutually exclusive (Catford et al. 2009), conceptually divergent measures may be valuable for different reasons. Thus, we examine each in turn, as understanding which of these hypotheses best explains exotic species spread is critical to the development of effective management policies.

Several authors have suggested that residence time may be an important factor in landscape spread of exotic plants (Gasso et al. 2009; Pysek and Vojtech

2005; Rejmanek 2000; Richardson and Pysek 2006). Because specific dates of introduction are often unknown, the term “minimum residence time” is frequently utilized (Rejmanek 2000) to describe the time elapsed since a species was first collected. One common way to determine minimum residence time (MRT) is through analysis of herbarium and collection data (Pysek and Vojtech 2005), or aerial photographs (Mullerova et al. 2005). When applied to specific taxa (Wu et al. 2003), hypotheses based on time alone can have low predictive power. In this regard, inclusion of many taxa may be required to estimate the importance of time in the distribution of introduced organisms and, to date, very few large-scale studies of this type have been conducted (Richardson and Pysek 2006).

In contrast, the relationship between biological traits and invasiveness has been studied extensively (Lloret et al. 2005; Rejmanek 2000; Smith and Knapp 2001) but with conflicting results. It has been suggested that invasion success is enhanced in species with biological traits similar to those of native species (Thompson et al. 1995), different from natives (Reichard and Hamilton 1997; Strauss et al. 2006), or some combination thereof (Hayes and Barry 2008; Rejmanek 2000). Moreover, research has been conducted on a wide variety of organisms to identify specific attributes that facilitate the spread and persistence of exotic species (for example, Kolar and Lodge 2002; Reichard and Hamilton 1997). Key characteristics (for example, ecological, biological, morphological, etc.) may very well enhance potential landscape spread of exotic plants but, while studies typically find combinations of traits that correlate with invasion success, consideration of biological attributes alone may be insufficient to explain or predict which exotic species will spread (Hayes and Barry 2008; Rejmanek 2000) unless these characteristics are broadly applicable to many different plant species. For example, elucidation of relationships between landscape spread and general life history traits or physiognomic classes would be useful because, while somewhat crude, this information is readily accessible for many species and relates directly to the interaction between organism and environment.

A growing body of literature suggests that invasion potential in new habitats may be correlated with an organism’s history of invasion elsewhere (Reichard

2000; Scott and Panetta 1993). Plants that are invasive in other regions are likely to become invasive when introduced into climatically similar areas (Crawley et al. 1996). Factors that influence persistence and spread of exotic organisms are not mutually exclusive, and include available habitat, time, and propagule pressure, although the relative importance of these factors is unknown (Wilson et al. 2007). In general, few studies have examined more than one or two factors at once (reviewed by Hayes and Barry 2008), and a major obstacle to comprehensive studies is the difficulty in gathering data on multiple factors for a large number of exotic species.

Given the large number of exotic plants found in most geographic regions, their long history of observation and collection, and the availability of data on their biological attributes, exotic flora provide an extraordinary opportunity to test these hypotheses. For some well-studied geographic regions it is possible to obtain accurate data on the dates of first collection and the current distribution of exotic plants. Here we jointly investigate the effect of MRT, biological traits, and history of invasive success on establishment and landscape spread of exotic plants. Specifically, we were interested in developing a general understanding of how plants spread across the landscape and how spread is related to commonly applied concepts of invasiveness. To do so we ask: (1) what are the historical and contemporary frequencies of introduction of exotic plants? (2) Is there a significant relationship between MRT and landscape spread? (3) Are rates of spread greater for taxa that are deemed invasive elsewhere or possess certain biological traits? (4) Is the landscape spread in one geographic region correlated with the landscape spread elsewhere? Moreover, we explore how the answers to these questions might contribute to the development of policies regarding control and management of exotic plants.

Methods

Data collection

We used herbarium data and collection records to develop comprehensive lists of exotic plants found in Michigan (Herman et al. 2001) and California (Hickman 1993). Species included in the study were

either observed or collected outside of cultivation. Data were collected in spring, 2007. The year of earliest collection was obtained by inspection of individual herbarium records for each species and records were considered from any location within each state. The difference between the date of earliest collection and 2007 provided an estimate of MRT. Our estimate is conservative because species may have been present prior to their first collection. Importantly, our data represent the state of two floras in 2007 and subsequent analyses in later years may yield different results due to natural spread of exotic species. With this consideration, data were used to test the effect of MRT on landscape spread.

The use of herbarium data to estimate MRT is well documented (Forcella 1985; Fuentes et al. 2008; Harris et al. 2007). Potential biases include identification ambiguity, accessibility of field sites, and variability of sampling efforts over time. These biases may be important when studying the spread of individual species over time (Delisle et al. 2003), but may be less relevant in broad comparative studies such as ours. Of these potential biases, variability of sampling effort over time may be accounted for statistically and we conducted a time-sensitive analysis to address this issue.

We used the number of counties with species occurrence as a measure of landscape spread (Arim et al. 2005; Forcella and Harvey 1988). For Michigan, distribution data were based on information originally published in *The Flora of Michigan* (Voss 1972, 1985, 1996) or by inspection of herbarium records, as in the case of newly introduced species or those that have undergone recent taxonomic revision. Michigan records examined are in the Michigan Flora database, housed at the University of Michigan Herbarium (Ann Arbor, MI). Data for exotic plants found in California (date of first collection and county-level distribution) were accessed online from the Jepson Interchange (http://ucjeps.berkeley.edu/interchange/I_treat_indexes.html). Records for Michigan and California are current to March, 2008.

To test the effect of biological attributes on landscape spread, we recorded the life history (annual, biennial, perennial) and physiognomy (forb, grass, woody) of all exotic species found in the two states. Attributes were assigned after an extensive literature review and are a subset of those suggested by Theoharides and Dukes (2007) and Hayes and

Barry (2008). Because life history and physiognomy are confounded, we combined these data and created a category termed ‘growth habit’, and all plants were classified as annual, biennial, herbaceous perennial, or woody perennial. Additional attributes, such as reproductive system, pollination strategy, and mode of dispersal, have been shown to correlate with landscape spread (Hayes and Barry 2008) and the importance of these findings is recognized. However, accurate data for these characters is not available for most of the species included in our study. Further, information is generally lacking for many newly introduced species and we were interested in assessing the utility of widely available, fundamental biological information.

In order to analyze the relationship between history of invasiveness and landscape spread, the Weed US Database (<http://www.nps.gov/plants/alien/list/a.htm>) was used to identify species considered invasive within the United States. This database is compiled from publications, reports, surveys, and observations, and lists plants that occur in natural areas in the US. Sources include local, state, and federal agencies, private non-governmental organizations and citizen’s groups, and universities. In order to account for the potentially confounding effect of including species known to be invasive in MI or CA in our analysis of history of invasiveness, analyses were also conducted after exclusion of species known to be invasive in each state (i.e. those on respective state invasive species lists). State designated invasive species were identified by the Michigan list of noxious and weedy species (http://www.michigan.gov/mda/0,1607,7-125-1569_16993-11250-,00.html) and the California Invasive Plant Council (<http://www.cal-ipc.org/ip/inventory/weedlist.php>).

Data analysis

Species records were summed by decade to assess the temporal distribution of invasion and to examine the cumulative sum of exotic plant species over time. Rate of landscape spread was determined by dividing the number of invaded counties by MRT. We created statistical models to evaluate the factors that influence spread. In all cases, landscape spread (number of counties where present-1) was the response variable. We conducted generalized linear mixed model

analysis of spread on MRT and examined covariance of two-way and three-way models. The following combinations of parameters were analyzed: MRT/life history, MRT/growth habit, MRT/history of invasiveness, MRT/life history/growth habit, and MRT/life history/history of invasiveness (PROC GLIMMIX; SAS Institute, Cary, NC). MRT was included in all models because of the expectation that species will spread with time, and to allow us to partition effects due to MRT and other factors. All two-way and three-way models included interaction effects. Model AIC was used to select models containing most information (or least information loss) among six models analyzed. Poisson and negative binomial are discrete probability distributions defined for random variables that take values equal to or greater than zero and are commonly used to model count data (Zar 1998). Preliminary model tests using AIC identified the negative binomial as most appropriate distribution for our data, and this distribution was used for subsequent analyses. In order to determine the amount of variation associated with specific model factors, we calculated likelihood-based R^2 -values as proposed by Nagelkerke (in Kreft et al. 2008).

Results

Exotic floras of Michigan and California

We recorded 943 exotic plant species in Michigan compared with 1131 in California, representing 34 and 14% of the overall flora in these states. Of the 20 families with the greatest number of exotic plant species in each state, 16 are shared between Michigan and California (see Supplemental Material I). Of these, the Asteraceae, Poaceae, Brassicaceae, and Fabaceae contain the most exotic species and comprise 38 and 45% of the total exotic flora of Michigan and California, respectively, suggesting the potential importance of phylogeny on landscape spread. However, presence or absence of native congeners was not significantly associated with landscape spread in either state ($F_{1,491} = 0.01$, $P = 0.94$ and $F_{1,751} = 0.91$, $P = 0.34$ for Michigan and California, respectively) even though rates of spread were variable by family (Supplemental Material I).

The first exotic plant collections occurred roughly 20–30 years earlier in Michigan (1822) than in California (1847). The distribution of peak introduction periods also differs between the two states ($P < 0.001$; $X^2 = 218.40$; $df = 15$), with the exception that both states display pulses during the latter part of the nineteenth and early twentieth century

(Fig. 1). Interestingly, peaks do not correspond closely with publication of major floristic studies (Michigan 1861, 1888, 1891, 1904, 1972–1996; California 1880, 1922–1923, 1959, 1993), suggesting that collection records reflect patterns of establishment, not simply collection effort. The mean numbers of exotic species that established per decade from

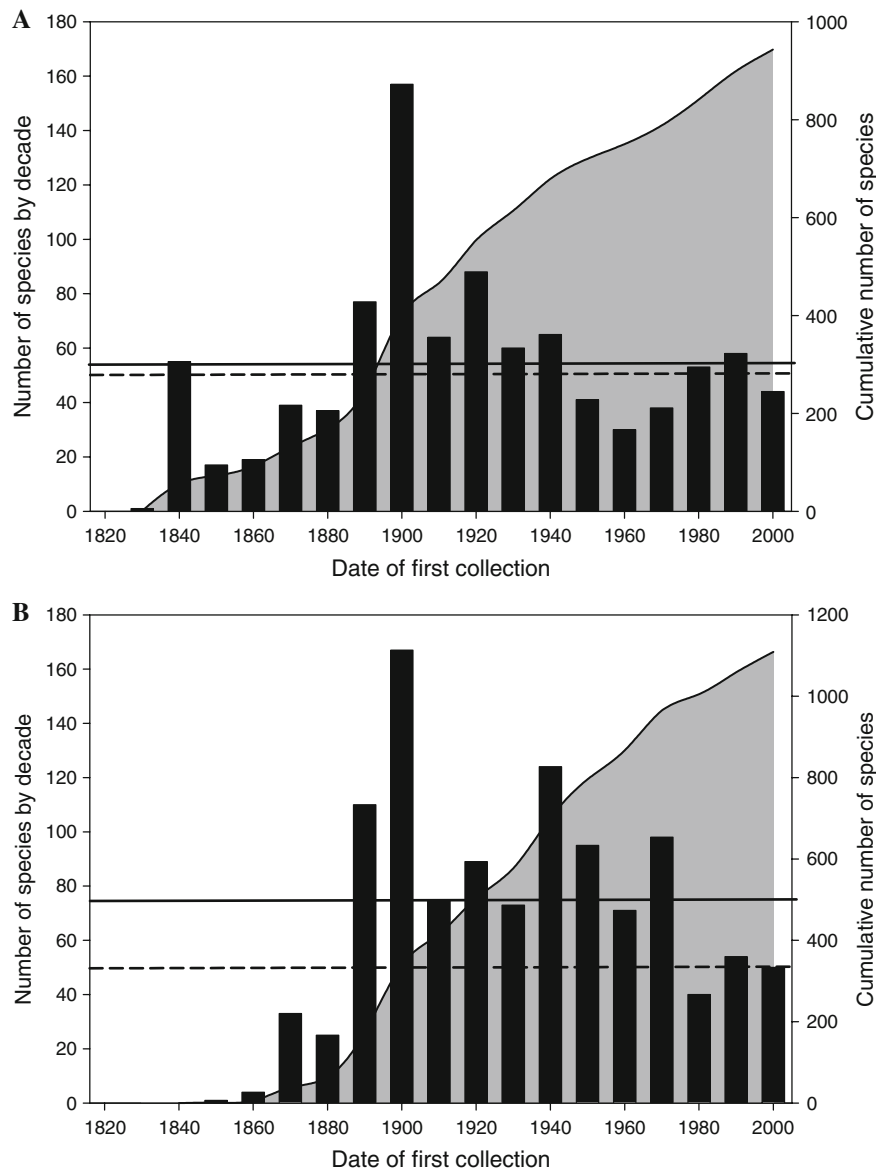
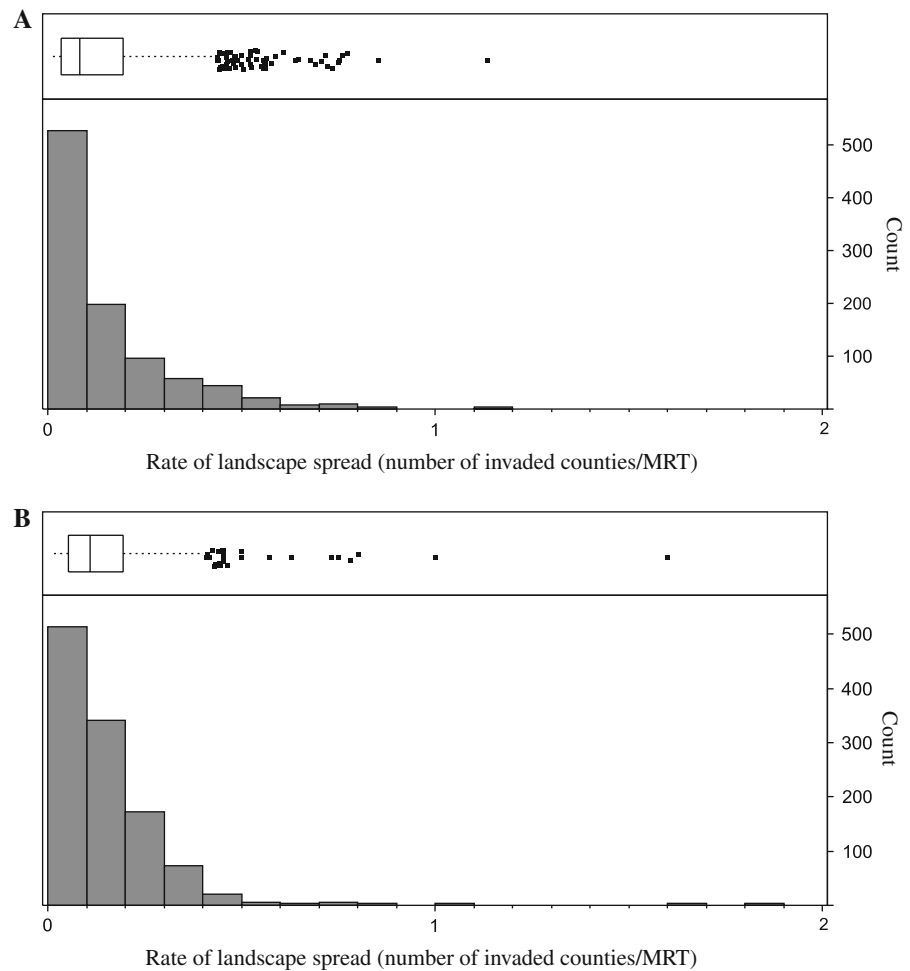


Fig. 1 Number of exotic plant species by date of first collection (used to determine MRT) in Michigan (**a**) and California (**b**) per decade (bars) and cumulative (line and shading) from 1820 to 2000. Overall mean rates of species

introduction per decade are 55.5 and 75.4 for Michigan and California, respectively (solid horizontal line); rates for the past three decades are 51.6 and 49.6, respectively (dashed horizontal line). Note differing scales for cumulative species

Fig. 2 Histogram and box plot for rate of landscape spread in Michigan (**a**) and California (**b**). Median rate for each state is represented by a vertical line inside the box (0.08 and 0.11 for Michigan and California, respectively), and the box spans the area between the 25 and 75% quartiles. Dots represent individual species



1820 to 2000 were 55.5 and 75.4 for Michigan and California, respectively, compared with 51.6 and 49.6 for the two states over the most recent three decades.

Michigan and California differ in overall size, elevation, temperature gradients, and history of human activity, but share remarkable similarities in patterns of exotic plant introduction and spread. An average of 50–75 exotic plant species per decade have been introduced into both states. While the frequency of introduction has declined somewhat in recent decades, nearly 50 species per decade were introduced in the last 30 years. Regarding rate of spread, the median number of counties invaded per year is similar for both states (Fig. 2; 0.08 and 0.11 for Michigan and California, respectively). In each state, only a small proportion of exotic plant species spread rapidly, defined here as those species found in greater than 25% of counties within 50 years of

introduction. The majority of exotics spread far more slowly with an average spread of just 3.2 and 6.3 total counties in Michigan and California, respectively, after 50 years. However, given sufficient time, the majority of exotic plants do exhibit landscape spread with a predicted time to reach 50% of counties in approximately 160 years for Michigan and 130 years for California.

Time, growth habit, and history of invasiveness

There is a strong positive relationship between MRT and landscape spread, as indicated by likelihood-based R^2 , in both Michigan and California (Table 1; Fig. 3). Although there is a significant positive correlation between the residuals associated with spread in Michigan compared with those for California ($P < 0.0001$), the magnitude of the correlation is

Table 1 Summary of model effects exploring landscape spread of exotic plants in Michigan and California

Model	Log likelihood	<i>k</i>	AIC	Δ_i	w_i	<i>R</i> -sq
Michigan null model	−3233.54	2	6471.08	511.18	0.00	NA
MRT [‡]	−3024.73	3	6055.45	95.55	0.00	0.36
GC [†]	−3244.14	3	6458.27	498.37	0.00	0.02
HOI [‡]	−3179.59	3	6365.17	405.27	0.00	0.11
MRT [‡] + GC + T × GH	−3017.67	5	6060.02	100.12	0.00	0.36
MRT[‡] + HOI[‡] + MRT × HOI	−2974.95	5	5959.9	0	0.98	0.42
MRT [‡] + HOI [‡] + GC [†] + MRT × HOI × GC	−2970.06	6	5968.12	8.22	0.02	0.43
California null model	−3836.05	2	7676.1	677.05	0.00	NA
MRT [‡]	−3534.09	3	7074.18	75.13	0.00	0.41
GC [‡]	−3800.56	3	7611.15	612.1	0.00	0.06
HOI [‡]	−3794.79	3	7595.57	596.52	0.00	0.07
MRT [‡] + GC [†] + MRT × GC [‡]	−3521.09	5	7060.17	61.12	0.00	0.43
MRT [‡] + HOI [‡] + MRT × HOI [†]	−3501.7	5	7031.39	32.34	0.00	0.45
MRT[‡] + HOI[‡] + GC[†] + MRT × HOI × GC[†]	−3485.53	6	6999.05	0	1.00	0.46
<i>State-listed invasive species removed</i>						
Michigan null model	−3066.37	2	6136.74	473.77	0.00	NA
MRT [‡]	−2871.01	3	5748.02	85.05	0.00	0.35
MRT [‡] + HOI [‡] + MRT × HOI	−2831.49	5	5662.97	0	1.00	0.4
MRT [‡] + HOI [‡] + GC + MRT × HOI × GC	−2823.03	6	5674.05	11.08	0.00	0.41
California null model	−2883.62	2	5771.24	538.77	0.00	NA
MRT [‡]	−2629.45	3	5264.9	32.43	0.00	0.43
MRT [‡] + HOI [†] + MRT × HOI	−2620.42	5	5250.83	18.36	0.00	0.44
MRT [‡] + HOI + GC [†] + MRT × HOI × GC	−2602.03	6	5232.47	0	1.00	0.46

The best model (as determined by AIC criteria) for each state is in bold. The null model compares the number of counties invaded to a negative binomial distribution in the absence of independent variables. Minimum residence time (MRT) is included in all models. For growth habit (GC), plants were designated as annual, biennial, herbaceous perennial or woody perennial; history of invasiveness (HOI) refers to taxa found on a comprehensive list of invasive species (see [Methods](#)). Significant effects ($P < 0.05$) are indicated by †, and highly significant ($P < 0.0001$) effects by ‡. Analyses represented in the lower portion of the table were conducted after removing species known to be invasive in each state; thus AIC values are not directly comparable with complete models. No models were considered competing (i.e. $\Delta I < 7$) with the best model for each state

small (Pearson's $r = 0.195$), suggesting that for individual exotic species, rate of spread in Michigan is only weakly related to the rate in California.

The number of exotic species found on the national list used in this study was similar for each state; 343 species in MI, and 374 species in CA. For two-way and three-way models of Michigan exotics, time and history of invasiveness were significant main factors affecting spread (Table 1). None of the interaction terms were significant. The best overall model for Michigan was the two-way combination of MRT and history of invasiveness. For California, MRT, growth habit, and history of invasiveness were highly significant in all two-way and three-way models. The best overall model for California exotics

included MRT, growth habit and history of invasiveness. Significant interactions for California exotics were observed between MRT and growth habit and time and history of invasiveness for two-way models. Interactions were also significant for the three-way model (Table 1).

History of invasiveness is a significant covariate with MRT in both states ($P < 0.0001$; Table 1; Fig. 4), with listed species having greater landscape spread in each state. In California, there is a significant interaction ($P = 0.006$), indicating that species with a history of invasiveness spread more quickly than those not known as invasive. The interaction effect was not significant for Michigan ($P = 0.31$) (Table 1; Fig. 4). These relationships are

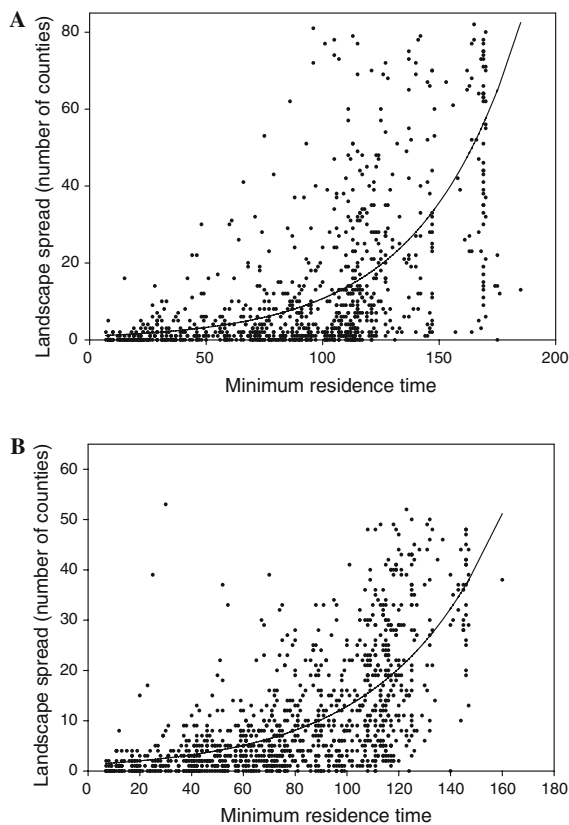


Fig. 3 Landscape spread (number of invaded counties) by minimum residence time (MRT, measured in years) for Michigan (a) and California (b). Dots represent individual species observations and lines represent predicted values generated by a model with time as the independent variable, landscape spread as the dependent variable, and a negative binomial distribution. Note differing scales for MRT

maintained when state designated invasive species are excluded from analyses. In Michigan, approximately 47 exotic species are listed as invasive, of which 75% occur in the state. In California, 260 exotic species are listed as invasive, and 87% of these are state residents. Species found on state lists that are currently not present in that state represent those targeted for exclusion via trade or other routes of introduction. For the subset of listed exotics that are present within a state, there is a significant relationship between MRT in California or Michigan and the percentage of species classified as invasive in each state (Fig. 5; Pearson's $\rho = 0.66$; $P = 0.0037$, and 0.89 ; $P < 0.0001$ for Michigan and California, respectively). Further considering the unintended

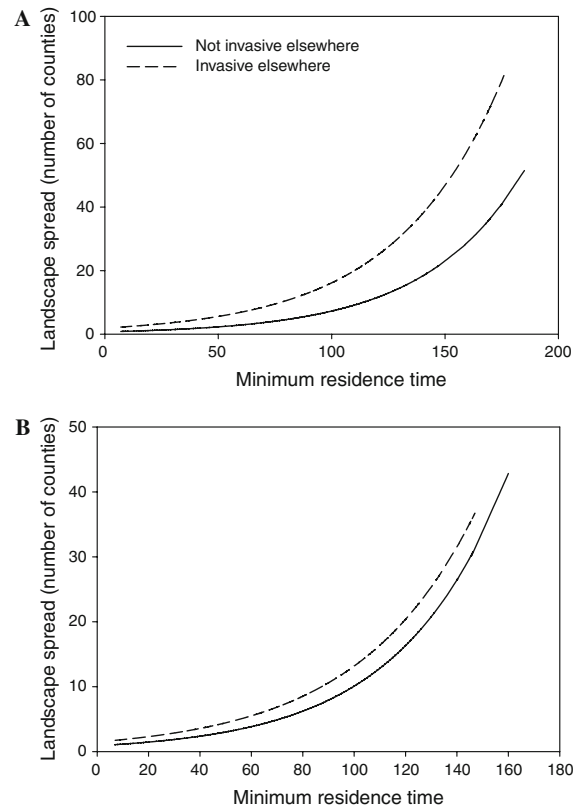


Fig. 4 Minimum residence time, landscape spread and history of invasiveness for Michigan (a) and California (b). History of invasiveness was categorized as presence or absence on a comprehensive US invasive species list, and species known to be invasive in each state were excluded from analyses (Michigan, $N = 910$ species; CA, $N = 904$ species). History of invasiveness is highly significant for MI ($P < 0.0001$) and significant for CA ($P < 0.0147$)

consequences of introductions, of those species with a MRT of 150 years, approximately 10–20% are deemed as problematic (appear on the state invasive plant list) in Michigan and nearly 40% in California (Fig. 5).

Discussion

Exotic floras of Michigan and California

The earlier dates of the first recorded exotic plants in Michigan may be associated with earlier settlement of Michigan relative to California. The Erie Canal opened in 1825 and Michigan became a state in 1836,

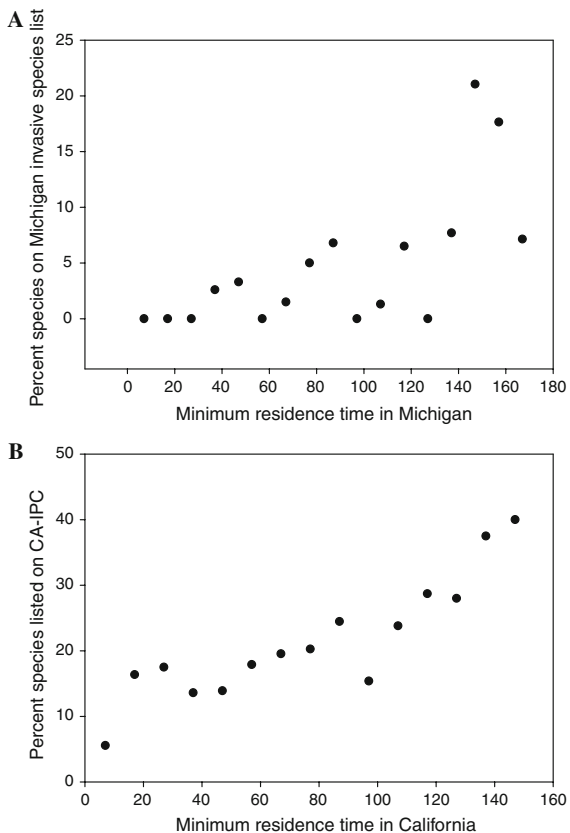


Fig. 5 Correlation between MRT and percentage of species that occur on the Michigan state list (a) and the California-IPC list (b). Pearson's coefficient = 0.66; $P = 0.0037$ for Michigan; Pearson's coefficient = 0.89; $P < 0.0001$ for California. Percentages were calculated per decade

while California statehood was granted during the Compromise of 1850, and the transcontinental railroad opened in 1869. Although the numbers of exotic species in Michigan and California are similar, Michigan has far more exotic plant species both per unit area and by percentage of the native flora than California. In addition to earlier colonization of Michigan, these differences between regions may be due to different disturbance regimes. In Michigan, historical disturbance is characterized by logging-mediated compositional change from conifer species to hardwoods (Abrams and Scott 1989), while contrasting fire regimes over the past 150 years is the major source of disturbance in California (although see Goforth and Minnich 2007; Keeley et al. 1999). Increased export of forest and agricultural products has been linked to spread of exotic plant species in Chile (Fuentes et al. 2008), and it is

likely that human-mediated disturbance facilitates spread of exotic plants in both Michigan and California (Corbin and D'Antonio 2004).

Time, growth habit, and history of invasiveness

Many previous studies have addressed factors that may affect spread of exotic plants (see review by Hayes and Barry 2008). These factors may be considered in two broad categories: (1) intrinsic factors that are related to specific characteristics of the species, and (2) extrinsic factors that are based on a priori, non-biological information. We explored one intrinsic factor (growth habit) and two extrinsic factors (MRT and history of invasiveness). Previous studies using herbarium records to determine the invasion potential of plants have focused on relatively few (1–10) species (Barney et al. 2008; Delisle et al. 2003; Mihulka and Pysek 2001) or on one physiognomic class (Harris et al. 2007). Retrospective studies of establishment and landscape spread have focused on well-known invaders (Barney et al. 2008; Mihulka and Pysek 2001), groups of species specifically chosen a priori (Harris et al. 2007; Reichard and Hamilton 1997), or some combination thereof. While these studies provide insight into invasion biology, they may be biased in that species chosen are already known to spread rapidly, significantly affect the environment, or both.

For Michigan and California, MRT is strongly associated with landscape spread. Given the myriad interactions potentially experienced by a species in a new habitat, the specific cause of this relationship is unknown. There is much unexplained variance in even our best models, and this could be due in large part to stochastic factors. Whether the relationship is driven by availability of habitat (for example, Barney et al. 2008), disturbance (Hobbs and Huenneke 1992), changes in land use (Fuentes et al. 2008), or some combination thereof remains a fertile area of study. Further, integrative approaches, such as those proposed by Catford et al. (2009), may be improved by inclusion of this parameter (Gasso et al. 2009, for example; Wilson et al. 2007).

Perhaps longer residence times provide increased opportunities for evolutionary changes which facilitate persistence and spread. Species disperse to maximize access to resources, minimize negative inter- and intraspecific interactions, access mates, or

combinations thereof. The speed at which species spread is mitigated primarily by dispersal ability (MacArthur and Wilson 1967) and Allee effects (Drake 2004) and, while spread of exotic plants may be mediated by both species richness and species composition of communities being invaded (Crawley et al. 1999), even diverse native communities are susceptible to invasion (Levine 2000). Wilson et al. (2007) argue the importance of propagule pressure and extent of suitable habitat, and it is likely these factors play key roles in landscape spread as well. Finally, lag times, possibly associated with hybridization and creation of novel genotypes (Ellstrand and Schierenbeck 2000, for example), are thought to play a role in the spread of exotic species. However, the significance of lag times remains sufficiently vague because this period is difficult, or often impossible, to measure under unmanaged conditions.

Harris et al. (2007) suggests that information about biological attributes and life history traits may offer strong predictive power. However, data from our study do not strongly support the sole use of biological traits for prediction of landscape spread of exotic plants. Related, while we found differences in rate of spread at the family level, the effects of biological traits and phylogeny on landscape spread is variable at different spatial scales (Cadotte et al. 2009, respectively; Hamilton et al. 2005) and may thus serve as a poor predictor of overall invasiveness. In general, our findings are similar to those reported by Castro et al. (2005) which suggest that historical factors may provide more consistent information about landscape spread than biological characteristics. Growth habit was significant only in California, where it explained a relatively small proportion of the variation in spread. The California pattern is driven by the relatively slow spread of woody plants and the relatively fast spread of annuals in that state. Also, grass and legume families are relatively abundant in the California exotic flora (Supplemental Material I), and this may affect the analysis of landscape spread by increasing emphasis on these groups. For example, exotic annual grasses are abundant in California and their effect on native ecosystems is well-known (Hamilton et al. 1999). It is also likely that land use change in California has contributed to shifts in species composition (Corbin and D'Antonio 2004), although some historic accounts of disturbance may be of dubious origin (Goforth and Minnich 2007).

State invasive plant lists are likely created to represent legislative priorities as well as biological and environmental concerns, and their composition represents these disparate influences. We found that 10–40% of species with MRT greater than 150 years in Michigan or California are deemed invasive in those states, respectively, and that this percentage increases with MRT. This finding is consistent with Williamson et al. (2009) who suggest that it takes at least 150 years for species to reach their maximum distribution over relatively large (10^5 km²) geographic areas. A high proportion of species introduced into Michigan and California before 1900 are now considered invasive. Perhaps this early period of introductions resulted in the transport and establishment of particularly invasive species, although time-sensitive analyses limited to data collected in the past 100 years identified the same best models for each state as were identified by full analyses (Supplemental Material II). Several of the early and widespread introduced plants in both states are forage grasses (e.g. *Dactylis glomerata*, *Phleum pratense*) that were undoubtedly intentionally introduced, while others are weedy species (*Digitaria sanguinalis*, *Echinochloa crus-galli*) that were unlikely to be intentionally distributed. We did not find a preponderance of forage or crop species among the early invaders, thus an alternative hypothesis is that 10–40% of all exotic plant species will be considered invasive given sufficient time. Given our data, it is not possible to know which of these explanations is most plausible and only time will tell what percentage of newly introduced species will become invasive. Regardless, these findings are in contrast to previously presented theories, such as the “tens rule”, which suggests that relatively few introduced species (10% of those that become established) become invasive (Williamson and Fitter 1996). Similar to Forcella (1985) and Williamson et al. (2009), our findings suggests that today's exotic weeds will become tomorrow's invasive species.

Implications

There are several distinct stages in the introduction process and our study provides a particularly robust analysis of processes involved with landscape spread. Exotic floras vary widely from the Great Lakes region to the West Coast, and examination of factors that

influence establishment and spread of exotic plants in these two vastly different regions provides an opportunity to determine whether general patterns determine invasion success, or instead, whether historical contingencies and local processes are more important. Considering the exotic floras of these two regions, we found that even a fundamental biological category such as growth habitat is a poor predictor of spread in these states. Rather, it is evident that time alone explains the greatest amount of variation and is characterized by initially slow, and then rapidly accelerating, landscape spread of exotic plants. The median rate of spread of exotic plants in Michigan and California is not rapid, and the initial slow spread suggests that there is considerable time for managers to act to contain or perhaps even eradicate newly discovered exotic species. Moreover, the absence of recently introduced, widely dispersed plants in both states suggests that current exotic introductions are following a similar pattern, such that many seemingly innocuous species are likely to eventually spread and be considered invasive in the future.

Our results suggest that, given sufficient time, many exotic plants will spread and be deemed problematic. Binding international agreements require use of science-based, transparent evaluation systems to justify exclusion of plants and plant products for importation (FAO 1997). Our findings encourage great prudence on the part of regulators and acknowledgement that importation decisions are continental in scope and are nearly irreversible. We endorse pest risk analysis (Federal Register 2009) for proposed new imports that evaluate the ability of species to spread outside of cultivation. Pest risk analysis should be coupled with enhanced efforts at early detection and rapid response to eradicate or contain newly established exotics or those in the very early stages of landscape spread. Mechanisms which may facilitate these approaches include collaborative state and regional programs to promote active surveillance by trained botanists, as well as citizen-focused education and stewardship activities.

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