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ORIGINAL ARTICLE

Can herbarium records be used to map alien species invasion and native species expansion over the past 100 years?

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ABSTRACT

Aim To determine if the temporal and spatial pattern of alien plant invasion and native plant expansion can be observed using 100 years of herbarium data from Oklahoma, USA, and to eliminate herbarium collection biases in such analyses.

Location Oklahoma, USA.

Methods Using herbarium records from the Oklahoma Vascular Plants Database from 1903 to 2004, we reconstructed the spatial and temporal collection history of two alien invasive taxa (*Lonicera japonica* and *Tamarix* spp.) and three native expansive species (*Ambrosia psilostachya*, *Amphiachyris dracunculoides* and *Juniperus virginiana*). To compare the overall collecting trend, groups of native non-expansive taxa were selected as counterparts. We recorded the year of the first collection in each township in Oklahoma for all taxa. The cumulative number of occupied townships was log-transformed, plotted against time and modelled with linear regression. The slope of the linear regression represented collection trend over time for the non-expansive counterpart group. However, for the invasive and expansive species, the regression slope represented the collection effort *plus* the invasion or expansion rate. We calculated the proportion of invasive and expansive species to non-expansive species by dividing the cumulative number of townships for each invasive or expansive species by the cumulative number of townships occupied by the counterpart group (proportion curve).

Results Maps of the collection records of invasive and expansive taxa illustrated no discernible spatial invasion or expansion pattern. The slopes of the linear regression for alien invasive taxa were significantly steeper than those of their associated native non-expansive counterparts, indicating an increase in abundance. *Juniperus virginiana*, *L. japonica* and *Tamarix* spp. exhibited one or more periods during which they were collected at a disproportionately higher rate than their native non-expansive counterparts.

Main conclusions Patterns of species invasion and expansion in Oklahoma were detected using techniques developed for regions with longer collecting plant histories. The proportion curve analysis eliminated some biases inherent in herbarium data by reducing the effect of collecting effort. Both the regression model and proportion curve analyses illustrate the temporal invasion patterns of alien invasive species. The native species did not show a clear expansion pattern. The information found in recently established herbaria may not be sensitive enough to detect the increase in abundance of native species.

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Keywords

***Ambrosia psilostachya*, *Amphiachyris dracunculoides*, collection bias, herbarium specimen, historical spread, *Juniperus virginiana*, *Lonicera japonica*, Oklahoma, *Tamarix*.**

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INTRODUCTION

Understanding the temporal and spatial dynamics of invasive and expansive species has become an important research topic for biogeographers, ecologists, weed scientists and conservation biologists. To understand the geographical history of alien plant invasions and native plant expansions many researchers are turning to the vast storehouses of information associated with herbarium specimens. Collections of alien plant species in herbaria around the world are being analysed to help ecologists recognize the spatio-temporal patterns of plant invasions (Stadler *et al.*, 1998; Delisle *et al.*, 2003; Woods *et al.*, 2005; Wu *et al.*, 2005; Barney, 2006; Chauvel *et al.*, 2006; Fuentes *et al.*, 2008). Herbaria are underutilized institutions that contain a large repository of historical and geographical information. Pyšek, using European herbarium specimens, developed a technique to quantify invasion rate (Pyšek, 1991; Pyšek & Prach, 1993; Mihulka & Pyšek, 2001; Pyšek *et al.*, 2003). He used the term 'invasion curve' to represent a regression model of the cumulative number of localities of an invasive plant plotted against the year of collection. The slope of the regression was considered a quantification of the invasion rate (Pyšek & Prach, 1993).

However, we must be cautious when interpreting regression models calculated from herbarium data because of the non-random sampling bias inherent in plant collections. Few studies take into consideration the biased nature of natural history collections such as: unequal sampling effort over time, non-random geographical representation, poor location information, incorrect identification, and disproportionately represented taxa. Therefore, methods must be developed to remove such biases to reveal the true pattern of invasion. Temporal variation in plant collection effort is apparent when the number of herbarium specimens is plotted against year. For example, in the herbaria of the state of Oklahoma, USA, the number of specimens collected per year since 1883 varies from zero to 6365, with a mean of 1752 per year (Hoagland *et al.*, 2006). The intensity of floristic inventory is therefore highly variable and this should be taken into account when studying invasive species. The increase in the number of specimens of an invasive species may indicate an increase in abundance, or simply may mean an increase in the overall collecting effort that year or decade. Mihulka & Pyšek (2001), using data from herbaria across Europe, corrected for collection rate among countries to account for the variation in plant collecting intensity. Delisle *et al.* (2003) also developed a method to account for the bias associated with temporal variation in plant collections in riparian areas of southern Québec, Canada. They selected widespread, native non-invasive species to provide a picture of collecting trends in the region. In addition to comparing collection rates, they calculated the ratio of invasive and non-invasive plant records for each year, termed the 'proportion curve' (Delisle *et al.*, 2003). If the proportion of invasive species collected increases over a period of time, this suggests that the invasive species increased in range or abundance. This differs from Pyšek's invasion curve, which evaluates the overall invasion rate of a species since its first collection and does not take into account specific time periods during which invasion may have occurred rapidly.

Pyšek also recognized that herbarium data have limitations and believed that a 'strong, long-term floristic tradition' in the region is important to produce reliable analysis of plant invasion (Pyšek & Prach, 1993). Yet, Fuentes *et al.* (2008) in Chile, Woods *et al.* (2005) in Kansas, USA, Delisle *et al.* (2003) in Québec, Canada, and Stadler *et al.* (1998) in Kenya all produced analyses with data sets that were significantly more recent than the several hundred years of data available in Europe. In Kansas the earliest specimen was collected in 1869, while in Québec the earliest specimen was collected in 1820. For Chile, Fuentes *et al.* (2008) only analysed the herbarium specimens collected since 1900. In Kenya a few specimens were collected before 1940, but most were collected after 1960. Wu *et al.* (2005) were concerned with the adequacy of using herbarium data to map the distribution of alien invasive species because of their short-term history in Korea. They studied *Crotolaria* species that had only been naturalized for 70 years. Not all European studies have the benefit of a long-term data set. Chauvel *et al.* (2006) examined the increase of North American *Ambrosia* species in France using only *c.* 150 years of data.

We were interested in testing these methods on herbarium data found in the Oklahoma Vascular Plants Database (OVPD), the repository for the plant collection data of the state of Oklahoma. The OVPD represents slightly over 120 years of plant collecting, with the earliest specimen collected in 1883, though significant numbers of plant collections were not made until the 1910s (Hoagland *et al.*, 2006). Not only are we interested in applying these methods to truly invasive species, but we are also interested in detecting the patterns of increase of native expansive species. Invasive taxa are alien species that have spread over a considerable area after introduction from another region by humans (Richardson *et al.*, 2007). Expansive species are native plants that are moving into new areas and increasing in abundance because of human-induced changes to the landscape. Some of the expansive species are considered to be agricultural weeds, but some, especially in the Great Plains of North America, are woody species encroaching on grasslands. In this paper we address the following questions: (1) Will we be able to detect the spatial and temporal invasion pattern of alien plants in Oklahoma using the relatively recent collecting history represented in the OVPD? (2) Can we effectively eliminate regional and temporal biases using previously developed research methods? (3) Will these methods be suitable for illustrating expansion patterns of native weedy plant species?

MATERIALS AND METHODS

We reconstructed the spatial and temporal collection history of: two alien invasive taxa; three native expansive species; and three native non-expansive counterpart groups using records in the OVPD. We chose taxa that are both alien and native to see if we would be able to detect a spatio-temporal pattern of increase from herbarium records. Nomenclature follows the PLANTS Database (USDA, NRCS, 2006). We selected four species and one genus that are considered 'weeds' in the Great Plains (Stubbendieck *et al.*, 1994; Southern Weed Science Society, 1998; Coppedge *et al.*, 2002; Friedman *et al.*, 2005; USDA, NRCS, 2006): *Ambrosia psilostachya* DC. (Asteraceae), *Amphiachyris dracunculoides* (DC.) Nutt. (Asteraceae), *Juniperus virginiana* L. (Cupressaceae), *Lonicera japonica* Thunb. (Caprifoliaceae) and *Tamarix* L. (Tamaricaceae). *Ambrosia psilostachya* and *Amphiachyris dracunculoides* are native to Oklahoma and are considered to be agricultural weeds (USDA, NRCS, 2006). *Juniperus virginiana* is a woody species native to Oklahoma that is known to increase in abundance in grasslands in the absence of fire (Coppedge *et al.*, 2002; USDA, NRCS, 2006). *Lonicera japonica* and *Tamarix* are alien invasive taxa that originated in Asia and Eurasia, respectively (USDA, NRCS, 2006). Species of *Tamarix* known to occur in Oklahoma are *Tamarix parviflora*, *Tamarix ramosissima* and *Tamarix chinensis* (Tyrl *et al.*, 2006). We grouped all species of *Tamarix* for our analysis due to the difficulties of identification, current confusion in the taxonomy and similar ecological functional roles.

To compare the overall collecting trend, groups of non-expansive species native to Oklahoma were selected as counterparts for each invasive or expansive taxon. Species chosen for counterpart groups were selected based on the following criteria: represented in the OVPD with at least 200 specimens; distribution similar to the invasive or expansive taxa; similar life-form or habit; readily identifiable; and not taxonomically confusing. We used a combination of several species to diminish possible collecting bias found in any particular species.

The following species in the Asteraceae were assigned to the non-invasive counterpart group for *Amphiachyris dracunculoides* and *Ambrosia psilostachya*: *Engelmannia peristenia* (Raf.) Goodman & Lawson, *Gaillardia pulchella* Foug., *Liatris squarrosa* (L.) Michx., *Pyrrhopappus grandiflorus* (Nutt.) Nutt. and *Ratibida columnifera* (Nutt.) Woot. & Standl. An effort was made to choose species within the same family, of approximately the same size and found in similar habitats. The following common, woody species were chosen as native non-expansive counterparts for both *J. virginiana* and *Tamarix* spp.: *Morus rubra* L. (Moraceae), *Prunus angustifolia* Marsh. (Rosaceae), *Rhus aromatica* Ait. (Anacardiaceae) and *Sapindus saponaria* L. (Sapindaceae). Similar to the invasive and expansive species to which they will be compared, these woody species are large shrubs or small trees and are widely distributed throughout the study area. We chose two congeneric species, *Lonicera flava* Sims and *Lonicera sempervirens* L., as native non-expansive counterparts for *L. japonica*. These were chosen based on similar taxonomy (within the same genus), habit (vining perennials), habitat (woodland edges and fence rows) and distribution (eastern Oklahoma). By comparing the temporal and spatial collection rates of invasive and expansive taxa with non-expansive taxa, we attempted to understand the general collecting trend so that attention could be drawn to the invasion and expansion history. We hope to de-emphasize the general collecting trend of the native non-expansive taxa from the collecting trend of invasive species to emphasize the increase in abundance over time of the invasive and expansive species.

All specimen records for invasive and expansive species and their non-expansive, native counterpart groups were selected from the OVPD, which includes all plant collections from the following major herbaria: OKL, OKLA, TULS, OCLA, CSU and DUR [for institution names and locations see Holmgren & Holmgren (2006) and Hoagland *et al.* (2006)]. At the time of this research, minor plant collections represented in the OVPD were from Oklahoma Panhandle State University at Goodwell and the University of Oklahoma Biological Station at Kingston. In general, herbarium specimens have the following associated data: species name, location of collection, collector, collection date and collector's collection number. However, there is no standard label format or data requirements, and many specimens lack even basic data. The variable nature of information provided on herbarium specimen labels required the elimination of some specimens from our study. First, specimens lacking a specific collection date were removed from analysis. Cultivated specimens were also removed from analysis. Specimens with unknown or imprecise location information were excluded from analysis. Specimens of the same species with identical collectors, collection dates, collection numbers and locations were considered duplicate records and treated as one collection.

Specimens in the resulting data set were georeferenced to township (93.3 km^2) and mapped using ArcGIS 9.1 (ESRI, Redlands, CA, USA). Townships, established in Oklahoma during the Public Land Survey of 1871, are quadrangles *c.* 6 miles (9.66 km) on each side and contain 36 equal sections (Hoagland, 2006). If not recorded, the township was determined by interpreting directions to collection location provided on the herbarium label. The date and location of the first collection in each township was identified and the total number of townships in which the invasive and non-invasive counterpart groups were found was calculated. For a better comparison of the uneven sample sizes of the invasive and expansive species with their counterpart groups, we log-transformed ($\log_{10}$) the cumulative number of occupied townships. Beginning with the first collection of the invasive or expansive taxa, the data were plotted against time, and linear regression models were calculated. The slope of the linear regression model was used to quantify the collection and invasion or expansion rate of the taxa in this study. The slope of the curve represented collection effort over time for the non-invasive counterpart group and collection effort *plus* invasion rate for invasive species. The steeper the slope of the curve, the faster the rate of collection or invasion (Pyšek & Prach, 1993). We then tested equality of the slopes of the regressions (Sokal & Rohlf, 1995). We also employed the method developed by Delisle *et al.* (2003) to compare the trend in general collecting of non-invasive species to the collection trend of invasive species because this method does not correct for the temporal variability of plant collections. We calculated the proportion of invasive to non-invasive plant collections by dividing the cumulative number of townships for each invasive species by the cumulative number of townships occupied by the non-invasive counterpart group. This proportion illustrated in graphical format, the proportional curve, allowed us to examine collection rate during short time periods.

RESULTS

Herbarium specimens

Following the removal of unusable and duplicate specimens, 3396 records remained for analysis (Table 1). Of those, township was recorded on the specimen label for 1103 records: 2293 were manually georeferenced. Although the first specimen used in this analysis was collected in 1903, relatively few specimens of taxa of interest were collected in Oklahoma before 1935.

Spatial and temporal distribution

The native non-expansive counterpart groups of woody species and Asteraceae taxa were found throughout Oklahoma and were not concentrated in any geographical region (Fig. 1a,c). The native expansive taxa, *Amphiachyris dracunculoides*, *Ambrosia psilostachya* and *J. virginiana*, were also not limited to a particular region of the state (Fig. 2a–c). *Lonicera* collections, both native and alien, were generally restricted to the eastern half of Oklahoma (Figs 1b and 2d). *Tamarix* was found across Oklahoma with the exception of the south-eastern corner (Fig. 2e).

The maps generated from specimen location information illustrated no discernible spatial invasion or expansion pattern by any of the invasive or expansive taxa; new localities in different regions of the state were collected simultaneously (Fig. 2). The earliest collections of *Amphiachyris dracunculoides*, *Ambrosia psilostachya* and *J. virginiana* were scattered across Oklahoma in a pattern that did not suggest an expansion front or radial expansion pattern (Fig. 2a–c). The first four collections of *L. japonica* were made in north-central Oklahoma in the 1930s (Fig. 2d). However, subsequent collections were scattered throughout the eastern half of the state and did not follow a radial pattern of invasion. The first *Tamarix* collection was made in the centre of the state in 1910. There was no apparent radial or linear (such as along a river corridor) invasion of *Tamarix* based on initial analysis of the early collections points (Fig. 2e). The lack of evidence of an invasion front could indicate that the alien species were first introduced to the state in multiple locations.

Invasion and expansion rates

The linear regression models for the native expansive species, *Amphiachyris dracunculoides*, *Ambrosia psilostachya* and *J. virginiana*, were not significantly steeper than the models of the associated non-invasive counterpart groups ($P > 0.05$; Fig. 3a–c). The regression models for both the alien invasive taxa, *L. japonica* and *Tamarix*, had significantly steeper slopes than the associated non-invasive counterparts ($P < 0.01$; Fig. 3d,e). This indicates that the rate at which *L. japonica* and *Tamarix* have been collected over the last 100 years has increased in comparison with the collection rate of their associated non-invasive counterpart taxa. Comparisons of the

Table 1 The number of townships in Oklahoma, USA, occupied by select alien invasive taxa, native expansive species and native non-expansive counterpart groups.

	Total no. specimens in OVPD	No. specimens used in analysis*	No. townships in which taxa were found	Year of first collection
Ambrosia psilostachya†	240	201	140	1913
Amphiachyris dracunculoides†	277	236	168	1913
Juniperus virginiana†	603	466	236	1913
Lonicera japonica‡	121	103	75	1936
Tamarix species‡	398	297	178	1910
Native non-expansive Asteraceae§	1002	859	463	1903
Native *Lonicera* species§	283	231	103	1913
Native non-expansive woody§	1201	1003	555	1906

The total number of townships in Oklahoma is 2098. Specimens were recorded in the Oklahoma Vascular Plants Database (OVPD), the repository for the plant collecting data of the state of Oklahoma.
*Specimens were removed from analysis if they could not be georeferenced, were missing collection year, were cultivated, or were duplicate collections.
†Native expansive species.
‡Alien invasive taxa.
§Native non-expansive counterpart groups.

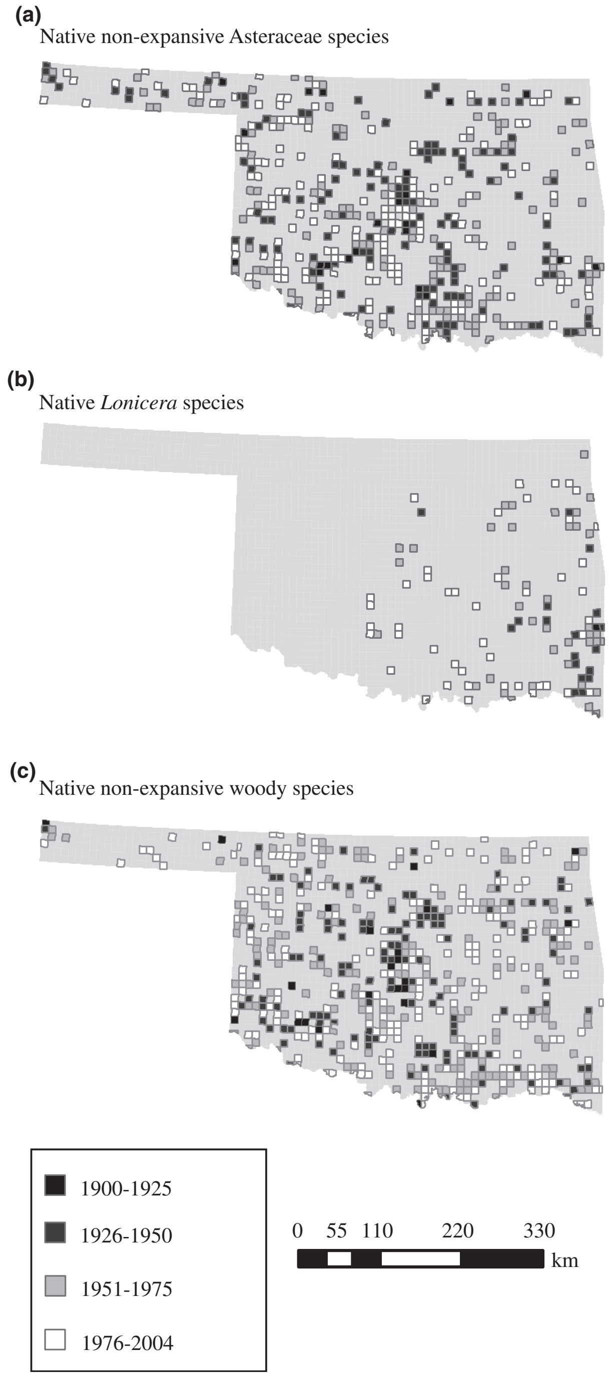

Figure 1 The spatial and temporal collection history of select native non-expansive groups in Oklahoma, USA. Occupied townships (9.66 × 9.66 km) are shaded based on the time period during which the first collection of that taxon was made. Darker townships are the locations of the earliest plant records.

regressions of *Amphiachyris dracunculoides*, *Ambrosia psilostachya* and *J. virginiana* with their native counterparts indicate that the collection rates of these species are not significantly different from the overall collection rate.

The proportion curve analysis indicates a time period during which some of the invasive and expansive taxa were collected disproportionately more compared with their native counterpart group (Fig. 4). *Juniperus virginiana* shows a likely increase in abundance during the 1930s, but, interestingly, appears to decline from that period to the present (Fig. 4c). *Lonicera japonica* has a dramatic spike after its initial collection in the 1930s and the proportion curve illustrates a steady increase in abundance relative to its native congeners since 1970 (Fig. 4d). *Tamarix* also increased in abundance in the 1930s and shows a slight increase during the 1960s (Fig. 4e). Neither *Amphiachyris dracunculoides* nor *Ambrosia psilostachya* have proportion curves that illustrate remarkable expansion, with the exception of a small, short increase in the late 1930s by *Amphiachyris dracunculoides* (Fig. 4a,b).

DISCUSSION

Regression models and proportion curves

Generally, after the initial introduction of an invasive species, the pattern of invasion begins with a lag period of few collections followed by a period of rapid, exponential expansion. Alien invasive species recently studied in France (Chauvel *et al.*, 2006), Kenya (Stadler *et al.*, 1998), Quebec (Delisle *et al.*, 2003) and across Europe (Pyšek & Prach, 1993) and North America (Barney, 2006) follow this temporal invasion pattern. Our data appear not to support a typical lag period because the short, flat portion of the curve at the beginning of the time period is also seen in the native non-expansive taxa. This suggests that the pattern is an artefact of collection history. The absence of a true lag period may be the result of the OVPD not having records during this phase of the invasion. The alien species in our study were both introduced to North America before many specimens in the OVPD were collected. The lack of a lag phase may also be due to the generation time (time for the population to reproduce) of the alien species in our research. Pyšek & Prach (1993) found that the generation time of riparian species affected the rate of invasion. The shorter a species' lifespan, the faster the invasion rate. The alien species examined in our research are both long-lived perennials, one a woody vine and the other a small tree/shrub. Both Pyšek & Prach (1993) and Delisle *et al.* (2003) were working with species in riparian areas, a habitat type that may see a faster rate of invasion. Water flow can be an important dispersal agent for both seed and vegetation fragments (Baker, 1974; Richardson *et al.*, 2007).

Despite the short and variable history of plant collection in Oklahoma, we found that the regression models indicate an invasion trend in the alien taxa (*L. japonica* and *Tamarix*). Both regression models had steeper slopes than their non-invasive counterpart groups, signifying over the past 100 years that the cumulative number of townships occupied was increasing faster than the number of townships occupied by non-invasive species. Delisle *et al.* (2003) found that four of the six invasive species in their study exhibited steeper slopes

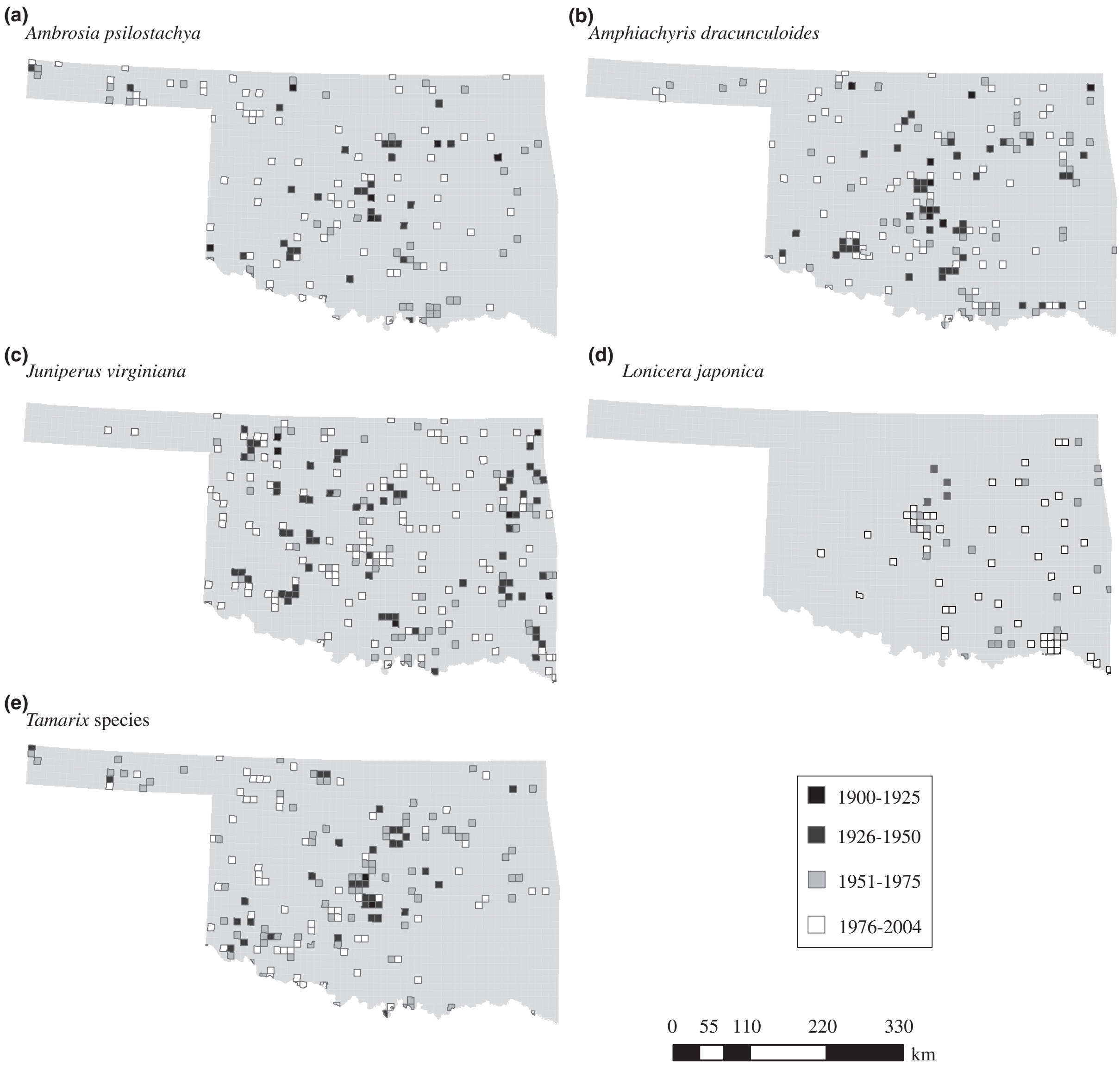

Figure 2 The spatial and temporal collection history of select alien invasive and native expansive taxa in Oklahoma, USA. Occupied townships (9.66 × 9.66 km) are shaded based on the time period during which the first collection of that taxon was made. Darker townships are the locations of the earliest plant records.

than their native counterpart groups. The expansion trend was not clear for the native expansive species that we studied. This may be due to the nature of native expansive species. Native expansive plants have presumably been present in the region since the arrival of Europeans in North America, but they have increased in abundance over time, in response, mostly, to human disturbance. In Oklahoma, this may be the result of a variety of factors, such as fire suppression, regrowth in abandoned fields or intensive grazing. By looking at native expansive species, we are really looking at an increase in population abundance which differs greatly from alien plant invasion. Attempting to use herbarium data to understand population dynamics of native species will be extremely difficult, if not impossible, due to the irregular nature of plant collecting and herbarium data.

The proportion curves revealed temporal invasion and expansion patterns, but at a finer scale, and therefore may better serve for analysis of data sets that cover a shorter time frame. *Juniperus virginiana*, *L. japonica* and *Tamarix* exhibited one or more periods during which they were collected at a disproportionately higher rate than their native non-expansive counterparts (Fig. 4c–e). Because the proportion curve of *L. japonica* shows an increase compared to that of the native congeners over the past 30 years until the present, we may hypothesize that *L. japonica* continues to invade new locations (Fig. 4d). The proportion curve for *J. virginiana* shows a significant increase in collections during the 1930s, but also has a steady decline for approximately the last 50 years. These results contradict other studies that clearly demonstrate that *J. virginiana* has expanded into grasslands in Oklahoma over

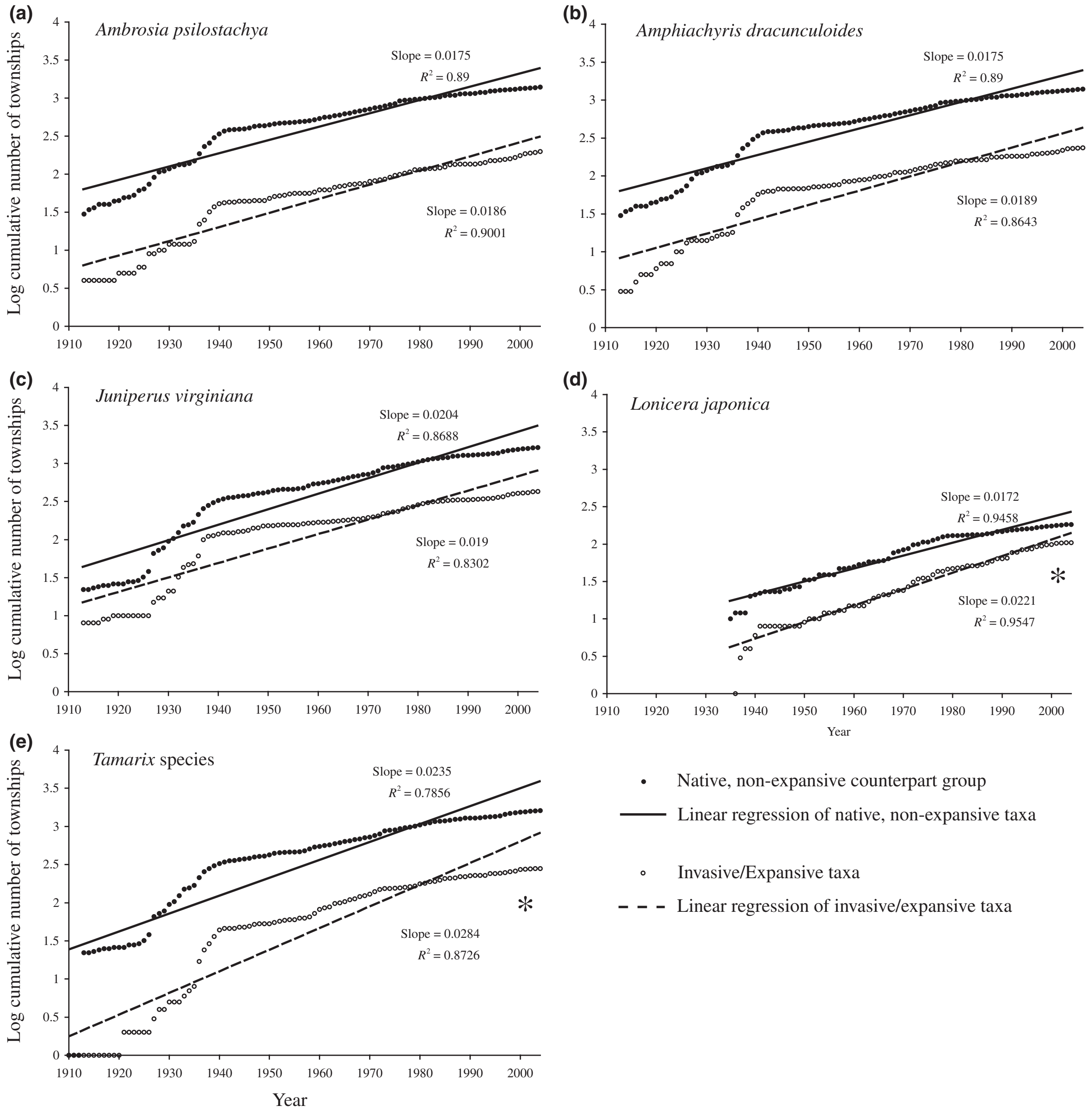

Figure 3 Invasion and expansion curves generated for select invasive and expansive taxa compared with the general collection trend of the native non-expansive counterpart group. For the non-expansive counterpart group the slope of the linear regression represented the collection trend over time. However, for the alien invasive taxa and native expansive species the regression slope represented the collection effort *plus* invasion or expansion rate. All linear regressions were statistically significant ($P < 0.001$). Regression pairs with * indicate slopes that differ significantly from each other ($P < 0.01$).

the past 50 years (Coppedge *et al.*, 2002). The differing results from the proportion curves of *J. virginiana* and *L. japonica* may be an indication of plant collector bias. The continued collection of *L. japonica* above the rate of its native congeners is evidence of the continued expansion of *L. japonica* into *new* locations. Plant collectors are interested in collecting species new to an area or rare in a habitat. The decline in *J. virginiana* collections with respect to other native woody species may be counterintuitive evidence of its increase in abundance. Botanists have generally neglected to collect native species considered to be abundant weeds. One of the most ubiquitous species in North America, *Taraxacum officinale* (the common dandelion), has only 202 records in the 210,000 records of the OVPD (Hoagland *et al.*, 2006). However, Woods *et al.* (2005) found that early collections of alien species in Kansas were extensive and were consistent with the overall collecting pattern for the state. The possible lack of interest in collecting native 'weedy' species makes analyses such as ours more complicated. While native expansive species may be ignored, alien invasive species may currently hold the interest of

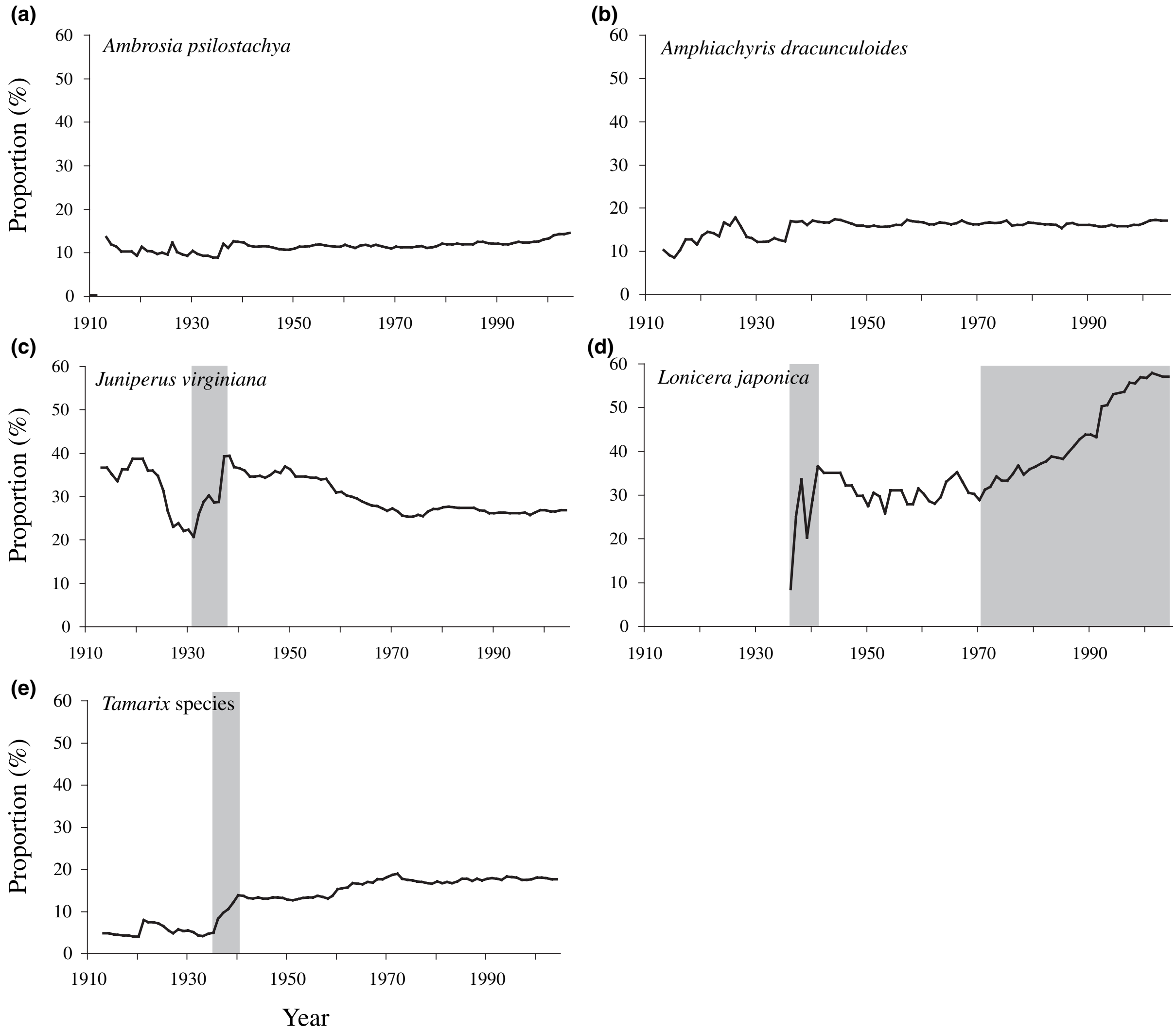

Figure 4 Proportion curves calculated by dividing the cumulative number of townships in Oklahoma for each alien invasive or native expansive species by the cumulative number of townships occupied by the native non-expansive counterpart group. Periods of increase, indicated by the shading, occur when the invasive or expansive taxon was collected more often than would be expected from the general collecting trend.

collectors who are trying to document their spread. The increase of *L. japonica* and *Tamarix* specimens in the past decade signifies the recent trend to identify and control alien invasive species and may not necessarily signify an increase in their real-world abundance.

Complications of herbarium data

The relatively short history of plant collecting in Oklahoma is problematic when one wants to understand long-term trends in the biogeography of the region, especially the invasion history of alien species. Pyšek & Prach (1993) believe that a long history of thorough plant collecting is necessary to produce reliable results. Initial collecting of the Oklahoma flora began late, when some alien species had already been introduced. Both *L. japonica* and *Tamarix* were introduced to North America in the early 1800s (Baum, 1967; USDA, ARS, 1970), well before the first herbaria were established in Oklahoma. However, this study demonstrates that the data from herbarium specimens in Oklahoma is sufficient to demonstrate periods of invasion by alien taxa. The history of plant collecting in Oklahoma may be too short for a detailed analysis of spatial patterns and population increase of native expansive species.

The nature of herbarium records, which involves opportunistic and non-systematic plant collecting, makes analysis difficult because this type of data gathering introduces several biases. Several historical events, beginning with the establishment of the state's universities, influenced the temporal plant collecting pattern of the records in the OVPD. The geographical pattern of plant collecting is determined by the preference of the plant collector, and is not based on a systematic grid of the state or stratified random sampling of ecoregions. Taxonomic bias – overrepresentation of certain groups of taxa – can be found in many collections. All temporal, geographical and taxonomic biases must be considered for one to be confident in the results obtained from herbarium data research. Through various methods we have made an effort to reduce the power of these biases to control our results.

Maps of plant distributions made with records in the OVPD should give us a reasonably accurate picture of the current extent of a given species within Oklahoma. Wu *et al.* (2005) tested the adequacy of herbarium data to illustrate the distribution of alien taxa. By comparing herbarium data with extensive field surveys, they found that herbarium records gave an accurate picture of the distribution and frequency of several species introduced into Korea during the last 70 years. Plant distribution maps will be more accurate as the number of plant collections increases. Therefore, the longer the history of plant collecting in a region, the better documented the flora and the more comprehensive the herbarium collections. The accumulation of specimens over 100 years should provide a good illustration of species distribution. Mapping the records from the earliest decades would be less likely to yield a reliable representation of species distribution because there are simply fewer specimens collected. Attempting to discern a pattern of invasion over time using the somewhat sparse data prior to 1930 is unlikely to represent the true invasion history of a plant; instead, we merely document the 'invasion' of Oklahoma by botanists. Given the short history of the herbaria embodied in the OVPD, analysis of the change in species distribution over time can be misleading. In reality, we did not find a spatial invasion pattern in the maps generated in our analysis. Neither of the alien taxa illustrates the pattern of species introduction and subsequent exponential spread via a front or corridor. This could indicate that the alien taxa were introduced prior to most collections in the OVPD or were introduced at multiple sites at approximately the same point in time. Delisle *et al.* (2003) and Pyšek (1991) found invasive riparian species dispersing along river corridors, but our maps of *Tamarix* gave little indication that it was spreading up or down riparian zones. We believe that *Tamarix* is almost certainly spreading along rivers in Oklahoma (DiTomaso, 1998); however, our data are not sufficiently sensitive, either temporally or geographically, to map the pattern. Baker (1974) described the typical North American invasion pattern to be scattered populations expanding to fill in absences between populations. Both the invasive alien and native expansive taxa in our study appear to follow this pattern.

The geographical distribution of specimens collected in Oklahoma is not random, but instead follows a pattern correlated with population centres and botanically 'interesting' areas. More species have been collected in counties with institutes of higher education than in neighbouring counties, though one would expect the flora to be similarly diverse (Hoagland *et al.*, 2006). Researchers in Kansas identified population centres as one of the problematic biases (Woods *et al.*, 2005), and Iverson & Prasad (1998) actually took into account the number of botanists residing in a county when they modelled the diversity of the Illinois flora. Locations of canyons, mountains, unique rock outcrops and other topographically outstanding elements have lured botanists to collect many specimens to document their distinctive flora. Counties with such features are overrepresented in the OVPD (Hoagland *et al.*, 2006).

Other biases can be found in collections. Concentration on a particular group of plants will produce a taxonomic bias. Many systematists deposit their collection of a single genus or species in a herbarium. Being knowledgeable about the region's history can also be useful. For example, certain prairie species may be overrepresented if they are part of roadside plantings organized by the Department of Transportation. Small projects, such as these, may be unknown and, alas, we cannot know all the nuances of bias in our data sets.

CONCLUSIONS

One could argue that the presence of too many uncontrolled variables in herbarium data sets leads to inaccurate representations of the historical biogeography of taxa. Nonetheless, the techniques developed by other biogeographers to analyse patterns of species invasion and eliminate biases inherent in herbarium data have been successful, to a degree, in our research. We deliberately chose taxa that are known to have increased in abundance and to be invasive in Oklahoma. We found that the alien invasive species demonstrate an invasion trend in both the regression model and proportion curve analyses. However, the native species that have been labelled 'expansive' did not show a clear expansion pattern. The information found in herbaria, especially comparatively recently established herbaria, may not be sensitive enough to detect the increase in abundance of native species in response to human disturbance, for example. Yet, herbaria are important storehouses of phytogeographical data. Unfortunately they are threatened institutions; plant collecting in the USA is in decline (Prather *et al.*, 2004), a trend confounded by a reduced interest in plant taxonomy (Wortley *et al.*, 2002), and herbaria have been eliminated at some universities in recent years. Herbaria represent many decades of plant collecting, thousands of miles travelled, and countless person-hours of identification. We hope research such as ours will encourage others to take advantage of information gathered by the scores of botanists before us and to design novel techniques and new avenues of research utilizing herbarium records.

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