

Metrics for macroscale invasion and dispersal patterns

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Abstract

Aim

The ability to quantitatively measure the continuum of macroscale patterns of species invasion is a first step toward deeper understanding of their causal factors. We took advantage of two centuries worth of herbarium data, to evaluate a set of metrics to measure macroscale patterns, allowing cross-species comparisons of invasive expansion across large geographic areas.

Methods

We used herbarium specimens to reconstruct county-level invasion histories for two non-native plants (*Alliaria petiolata* and *Lonicera japonica*), with distinct spatiotemporal distribution patterns over the past two centuries. Using county centroids from species' initial occurrences, we quantified point pattern metrics from multiple disciplines (e.g. urban crime analysis, landscape ecology etc.) that are historically used at smaller spatial scales, to evaluate their ability to detect macroscale spatial diffusion and amount of directional expansion. Metrics were further assessed for their ease of use, data requirements, independence from other metrics and intuitiveness of interpretation.

Important Findings

We identified four suitable metrics for distinguishing differences in spatial patterns: (i) standard distance, (ii) number of patches, (iii) Euclidean nearest neighbor summary class statistic coefficient of variation and (iv) mean center that when applied to county-level presence data allowed us to determine the directions by which distributions expanded and if distributions increased via outward expansion, infilling and/or jump dispersal events. These metrics when compared during the same invasion phase are capable of quantifying macroscale variability among species in their distributional and dispersal patterns. Being able to quantify differences among species in these patterns is important in understanding the drivers of species dispersal patterns. These metrics therefore represent a simple yet thorough toolset for achieving this goal.

Keywords: *Alliaria petiolata*, diffusion, herbarium, jump dispersal, *Lonicera japonica*, plant invasions

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INTRODUCTION

Patterns of ecological processes across large geographic areas emerge from complex, cross-scale interactions among many biotic and abiotic factors. This complexity inevitably contributes to macroscale patterns of species distribution and dispersal. Understanding the factors that contribute to these patterns has long interested various sub-disciplines of ecology such as paleoecology and biogeography (Matthew 1914; Dobzhansky 1950; Pianka 1966), and more recently macrosystem ecology (Fei *et al.* 2016), and is becoming more crucial for understanding macroscale patterns of a leading component of global change—biological invasions (Mooney and Cleland 2001; Strayer *et al.* 2006; Ricciardi 2007; Iannone *et al.* 2015). As a beginning step of understanding what drives macroscale dispersal patterns, one must first be able to effectively quantify

various characteristics of species expansion patterns both over time and across large geographic areas. Understanding these expansion patterns is critical for the proactive mitigation and control of newly invaded, rapidly expanding species.

Species distributions change via a series of diffusion and jump dispersal events (Shigesada and Kawasaki 1997; Wilkinson 2001), leading to the continued evolution of spatial patterns over time (see Fig. 1 for examples). Being able to quantify the variability in these changing spatial patterns, along with the directional movement and rates of spread, can help to reveal differences and similarities in patterns at different invasion stages of a given species and among different species. The quantification of these patterns, when paired with further consideration of species traits and environmental conditions, can provide increased understanding into the factors contributing to species expansion

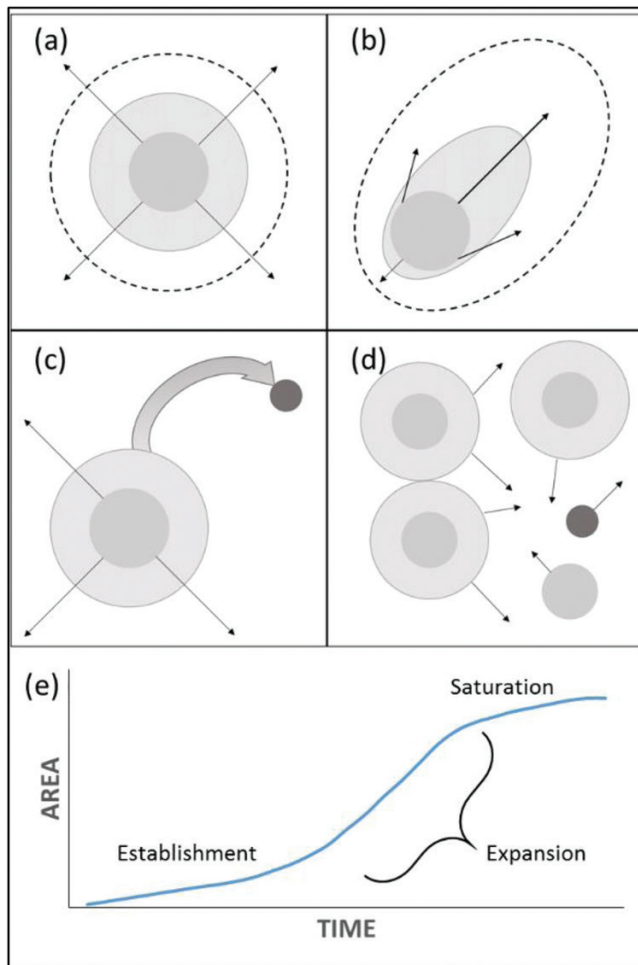


Figure 1: typified patterns of species expansion, including (a) radial diffusion from initial point of introduction; (b) directional radial diffusion due to barriers or environmental constraints; (c) a combination of radial diffusion and jump dispersal events; (d) initial dispersal to multiple satellite colonies from which diffusion and range expansion occur; and (e) establishment, expansion and saturation phases of invasion as determined by changes in rates of spread.

(Rouget and Richardson 2003). Despite the many indices developed to quantify spatial patterns, there is likely no single metric able to completely encapsulate the complexities of large-scale dispersal patterns (Pysek and Hulme 2005). The quantification of spatiotemporal changes in species distributions across large geographic areas will likely require multiple metrics that together are able to track changes in density, directionality and the velocity of the expansion. Identifying these metrics, however, is challenging due to the lack of long-term spatiotemporal data pertaining to species distributions.

The main objective of this investigation is to identify a set of metrics applicable to macroscale pattern recognition of invasive plant species expansions using methodologies already tested at smaller scales. The utility of these indices will be evaluated using collected herbarium specimen supplied spatiotemporal data for two invasive plant species, *Alliaria petiolata*

(M. Bieb.) Cavara and Grande (garlic mustard) and *Lonicera japonica* Thunb. (Japanese honeysuckle), which exhibit distinctly different macroscale patterns of spread and represent two common invasion trajectories, accidental and ornamental use. Historically, herbarium specimens have provided researchers with a wealth of knowledge concerning the taxonomy, systematics and evolution of collected plant material. Recently, the usage of these collections has been amplified into genetics, spatial ecology and climate change (Lavoie 2013). In this study, we also want to highlight the use of herbarium collections in understanding macroscale invasion patterns and processes, both spatially and temporally.

The outcomes of this investigation will provide a set of metrics that can be used at macroscales to quantify spatiotemporal patterns of plant species dispersal, which can aid better understanding of their spatial patterns, and perhaps of other ecological processes. These findings can also be used to aid the predictions of newly arrived or future invasions, which is of practical utility given the contribution of these species to overall global change (Vitousek et al. 1997; Simberloff 2011; Fei et al. 2014).

MATERIALS AND METHODS

Data selection and acquisition

To estimate patterns of spread for both species, we determined the timing of county-level presence of each invader for the eastern USA by using herbarium records we compiled covering the past two centuries. Each species exhibited variable rates of spread over the courses of their invasion histories, allowing us to identify different phases of their invasions (see Fig. 1e for definition of invasion phase). Specimens for *A. petiolata* and *L. japonica* were collected from ~120 differing herbaria and other published sources (see online supplementary Table S1 in Appendix S1). Following protocols by Delisle et al. (2003), specimens lacking locations, dates or which were obviously cultivated were discarded, and the species was considered to persist in a county once it was collected there. Historically, herbarium specimen records have been shown to be a viable proxy for species range and expansion data (Pysek and Prach 1995; Aikio et al. 2010a) and have also been used successfully to reconstruct the timing and extent of invasion (Barney 2006; Fuentes et al. 2008; Kannan et al. 2013). While herbarium data are known to exhibit both spatial and temporal bias due to non-random sampling efforts (Loiselle et al. 2008), the purpose of our study was to describe and differentiate spatial patterns and not to calculate specific spread rates of the actual species invasions, affording us the ability to assume these biases to cause minimal effects on the results.

Each of the species has a long invasion history in the USA, being introduced in the early 19th century (Munger 2001; Schierenbeck 2004). *Alliaria petiolata*, an upright obligate biennial forb, is believed to have been introduced in and around New York for use as a garden herb and medicinal purposes (Munger 2001). Due to its prolific seed production

(Nuzzo 1999), and its primary mechanism of dispersal by epizoochory (Cavers *et al.* 1979), its recent spread is believed to be mostly accidental (USDA 2016). In contrast, *L. japonica*, a perennial flowering vine, was introduced in multiple distant locations from New York to Louisiana, by way of the horticultural trade due to its fragrance and ease of growth (Lemke *et al.* 2011). The variability between these species in their growth forms, modes and number of introduction points, and life-history traits likely influences their invasion trajectories and current range sizes (Moravcová *et al.* 2015).

Metrics

Spatiotemporal dynamics of a species' range expansion encompasses a vast continuum of spatial patterns that lie within the general bounds of diffusion (i.e. gradual and regular spread, radiating in concentric circles) and jump dispersal (i.e. long distance spread to locations outside of a species current range) (Pielou 1979; Simberloff *et al.* 1997). To capture the entire gamut of potential spatial patterns in range expansion and infilling, it is essential to have metrics that measure both the density of, and the distances among, species observations. In addition, to determine if spatial patterns of expansion vary among invasion phases, we need a quantitative method for detecting abrupt changes in rates of spread, which likely signify points in time where these phases begin and end. This distinction among invasion phases can also help to ensure that comparisons among species in spatial patterns occur during the same invasion phases, making these comparisons more meaningful (Theoharides and Dukes 2007). Furthermore, to ensure the greatest utility and applicability of these metrics, we chose metrics (Table 1) assessing for ease of use, data requirements, independence from the other metrics, intuitiveness and their ability to distinguish spatiotemporal patterns at the macroscale.

To estimate the years at which the species' expansion rates changed, we performed a segmented linear regression (SLR) on the species expansion area (cumulative counties) versus time. This graph and its coinciding segmented regression thus depicted each species' invasion curve (*sensu* Pyšek and Prach 1993). The final recorded number of counties invaded by the two species differed considerably ($n = 581$ for *A. petiolata* and $n = 1075$ for *L. japonica*). Therefore, we unit-base normalized the county collection data prior to regression analysis to facilitate cross-species comparison using the following equation (x = cumulative counties):

$$X' = \frac{X - X_{\min}}{X_{\max} - X_{\min}} \quad (1)$$

To estimate the degree to which distributions were dispersed throughout a species' range and the directional migration of each species, we utilized two distance-based spatial statistic metrics: standard distance (STD) and mean center (MC). We calculated these metrics from the latitude and longitude (x , y coordinates) of the centroid locations of the counties from

which herbarium specimens were collected. The STD metric estimates the radius of the circle that encompasses 1 SD of our sample points, i.e. centroids of the invaded counties. MC of the distribution is calculated from the average of the (x , y) geographical coordinates of all the input points (in our case county centroids) at each time period (see Table 1). We measured the Euclidean distance between the original geographical center of the distribution, i.e. the centroid from which the invasion started, and succeeding decadal calculations of the MC coordinates to track the overall shifting 'weight' of the species distribution through time.

By using kernel density estimation (KDE) on the county centroids, we produced a smoothed raster surface reflecting the areas of higher density of collected specimens. Although wildlife studies often use 95% kernel density as the designation of the normal home range (Seaman and Powell 1996), 95% is thought to overestimate the range, and it has been suggested that between 50% and 80% is ideal (Borger *et al.* 2006). Percent volume curves (PVC) were constructed (Geospatial Modeling Environment, Version 0.7.3.0), and the 75% kernel density was chosen to represent the range density as it neither excluded all the peripheral samples nor extended beyond the convex hull of the known occupied area. This procedure enabled us to identify and then quantify true expanding colonies versus an outlying single collection. Using the KDE patches, two density-based metrics were calculated: coefficient of variation of the Euclidean nearest neighbor (ENN_CV) and the number of patches (NP). These metrics were then used, respectively, to identify jump dispersal events and to estimate intra-range species dispersion. The coefficient of variation is a ratio of dispersion that shows the extent of variability of the sample in relation to its mean (in our case, the measured Euclidean distances between the KDE patches at that time), and is calculated by taking the standard deviation of a frequency distribution and dividing it by the mean of that same distribution (i.e. s/\bar{x}). The metric number of patches (NP) is a simple count of the count of discrete KDE patches that are formed at the 75 PVC during each time period.

We also explored the utility of numerous other metrics (see online supplementary Table S2 in Appendix S2), but for multiple reasons found them to be less applicable to macroscales. We chose segmented regression over others' techniques (Liebhold *et al.* 1992; Mihulka and Pyšek 2001; Tobin *et al.* 2007; Aikio *et al.* 2010b; Gilbert and Liebhold 2010; Larkin 2012; Liebhold *et al.* 2013) because of its ability to detect changes in rates of spread, and thus transitions between different invasion phases (e.g. Fig. 1e). We also measured point distances between the centroids of all invaded counties and evaluated the effectiveness of using the maximum, mean and standard deviation of those distances as metrics of spatial dispersion. These metrics were not chosen, because relative to STD, they did not provide a significant improvement in pattern description and they required more data and computational time. Additionally, we investigated other metrics aimed

Table 1: metrics used to quantify macroscale patterns of spread including their equations and specific use

Metric	Abbreviation	Equation	Purpose
Regression slope	SLR	$\beta_1 z_i + \beta_2 (z_i - \varphi) + \dots$ Per (Muggeo 2008)	β_1 is the left slope, β_2 is the difference-in-slopes, and φ is the breakpoint. Variable z is normalized cumulative counties
Standard distance	STD	$SD = \sqrt{\frac{\sum_{i=1}^n (x_i - \bar{X})^2}{n} + \frac{\sum_{i=1}^n (y_i - \bar{Y})^2}{n}}$ Per (Environmental Systems Research Institute 2014)	x_i and y_i are the coordinates for feature i , $\{\bar{X}, \bar{Y}\}$ represent the mean center for the features, and n is the total number of features. Measures the dispersion around the mean center, a geographic standard deviation of points, i.e. county centroids, used to assess the degree of scatter for a distribution
Mean center	MC	$\bar{X} = \frac{\sum_{i=1}^n x_i}{n}, \bar{Y} = \frac{\sum_{i=1}^n y_i}{n}$ Per (Environmental Systems Research Institute 2014)	x_i and y_i are the coordinates for feature i and n is the total number of features. Average x and y coordinate of all represented points of a species distribution. Distance between succeeding MCs detects directional movement in consort with STD
Number of patches	NP	Count	The number of kernel density patches. Aggregation is revealed by the decreasing number of patches through time, indicating coalescence
Coefficient of variance of Euclidean nearest neighbor	ENN_CV	$CV = \frac{SD}{MN} (100)$	Standard measure of relative variability of inter-patch distances. Spikes in value identify a new colony with high variation in distance from others indicating possible jump dispersals

at quantifying aspects of area and edge, shape complexity and aggregation. We opted not to utilize these landscape-level metrics because either they were incapable of detecting spatial variability in our presence/absence data at the much larger spatial extent of our investigation or they were less intuitive.

Spatial metrics were calculated for decadal time intervals. Segmented regressions were conducted using the Segmented package in R (Muggeo 2008; R Core Team 2015). KDE and all distance geographic metrics were calculated using the Albers equal area conic projection (USGS) and ArcGIS 10.2.2 (Esri, Redlands, CA, USA). Landscape metrics were calculated utilizing FRAGSTATS (v4.2.1.603) (McGarigal et al. 2012). The final set of five metrics were verified for independence (see online supplementary Fig. S3 in Appendix S3), and the four spatial metrics were normalized from 0 to 1 to facilitate cross-species comparisons [see equation (1)].

RESULTS

Thresholds and rates of spread

Assisted by SLR, we found two invasion phases for *A. petiolata* (Fig. 2a) and three possible invasion phases for *L. japonica* (Fig. 2b). The first two line segments for the invasion curves of both species likely signify establishment phases. This distinction is due to both the relatively lower slope values for these line segments and the paucity of herbarium specimens collected during these periods. The subsequent segments, where rates of expansion increase, likely signify expansion phases. *Alliaria petiolata* showed a tripling in its rate of spread after 1960, which it still maintains. Comparably, the non-scaled counts show *L. japonica* accumulated 25 counties per year during its expansion phase versus *A. petiolata*'s

nine counties per year, but *L. japonica* only maintained that rate of spread for ~20 years. After that period *L. japonica*'s rate of spread declined, suggesting it is approaching a saturation phase. SLR revealed comparable values in the rate of spread for both species during their establishment phase, and the species' shift to expansion phase occurred in close time proximity to each other. Yet, the differences in normalized rates of spread during expansion phase that we detected (0.015 normalized units for *A. petiolata* and 0.025 normalized units for *L. japonica*) allowed us to investigate whether varying rates of spread would affect the utility of our spatial metrics.

Diffusion and jump dispersal

The four distance- and density-based spatial metrics were able to quantify where along the expansion continuum species exhibited diffusion and jump dispersal-like events. Additionally, they were able to differentiate these patterns between our investigated species. Increases, decreases or steady values of STD radius over time can provide evidence as to whether the expansion of a species is occurring as range growth or infilling. For instance, the continually increasing STD exhibited by *A. petiolata* (Fig. 3a and c) is the result of this species' distribution growing outward from a single foci introduction point located in the northeastern USA (e.g. Fig. 1b). On the other hand, *L. japonica*'s STD declines through the 20th century (Figs. 3a and d) owing to the species distribution diffusing from multiple introduction points located widely throughout its geographic distribution (e.g. typified by Fig. 1d). When a species distribution infills more than it expands, such as with *L. japonica*, STD values decrease (Fig. 3b).

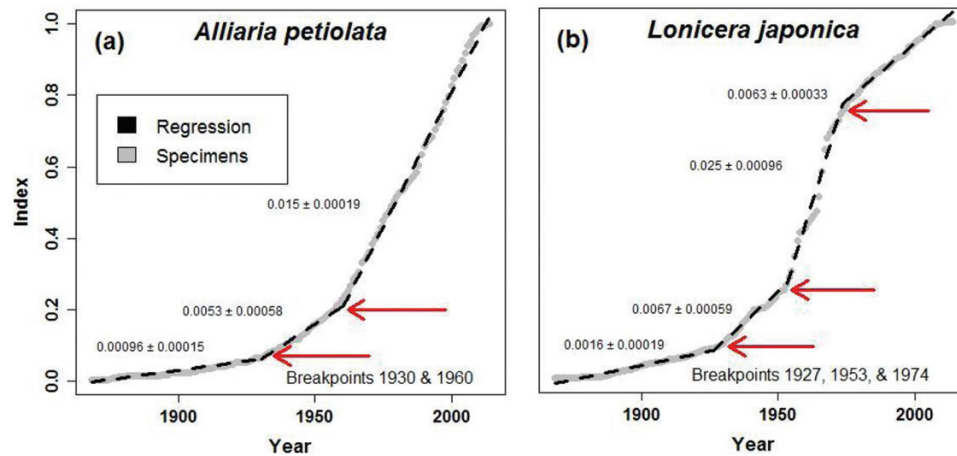


Figure 2: results of segmented linear regressions with scaled slopes \pm SE values revealing (a) establishment and expansion phases for *Alliaria petiolata* and (b) establishment, expansion and potentially saturation phases for *Lonicera japonica*.

We found both species experienced initial increases, followed by decreases, in the degree of spatial dispersion exhibited by their distribution. This pattern is revealed by the initial increase and then later merging of the kernel density patches (NP) (Fig. 3e and f). The NP metric allows investigation of the species' tendency to enlarge its territory either by more dispersed colonies or by the expanding colonies growing together into clumps. This knowledge used with the results from STD is able to distinguish overall long-term changes in dispersion. Both *A. petiolata* and *L. japonica* show an increase in NP from their initial colonization until the maximum NP count occurs during the transition from the establishment to expansion phase (Fig. 3c and d). Throughout their expansion phase, the NP values for both species continually decrease, showing patch coalescence into larger, less numerous colonies. *Lonicera japonica*'s NP values plummet, while those of *A. petiolata* continue to maintain moderate values. The plummeting NP values of *L. japonica* are largely due to increased density from infilling of the species' range (Fig. 3f). The moderate yet stable NP values of *A. petiolata* are due to the balancing of new patches occurring over time as this species' range expands westward, while older patches simultaneously merge together (Fig. 3e).

Utilizing the coefficient of variation from the measured Euclidean nearest neighbor distances (ENN_CV) calculated between the kernel density patches, we were able to detect instances of jump dispersal-type spread within the history of *A. petiolata*, but not in the history of *L. japonica*. Using the Euclidean nearest neighbor distances between all patches as our frequency distribution, abrupt spikes in the values of ENN_CV reveal the existence of a new patch with high variation of distance between the others. This indicates either a new introduction at a far distance or a genuine jump dispersal event. As an illustration, before being normalized to facilitate comparisons between species, if the calculated ENN_CV of the measured distances is $>100\%$, it indicates that the largest

distance between patches is more than double the overall mean inter-patch distance (McGarigal *et al.* 2012). The two spikes in value seen within *A. petiolata*'s history (Fig. 3c) arise from measured ENN_CV values of 116% and 143%. These instances of high values signify the appearance of patches far away from all others, and thus an indication of jump dispersal, such as the outlying patches resulting from *A. petiolata*'s westward expansion.

Directional expansion

Movement through time of the MC location of the distribution of each species revealed the directional trajectory of its expansion. The graph of the MC distances from first collection point of *A. petiolata* shows a continual linear increase indicating persistent expansive movement away from its initial location, while that of *L. japonica* shows a rapid decline in directional movement after 1960 (Fig. 3a–d). While the continual migration of the MC away from a species' introduction point indicates directional movement, a stationary MC requires further investigation. Stationary MC values can either be indicative of a range infilling, as seen in *L. japonica*'s later years (Fig. 3e and typified in Fig. 1d), or stem from equal expansion in all directions radiating outward from a species' initial introduction point. During *L. japonica*'s recent history, and most current invasion phase, all four spatial metrics (STD, MC, NP and ENN_CV) level off, while the rate of spread decreased (Fig. 2b), suggesting the distribution of this species to be stabilizing. Alternately, if a species is expanding equally in all directions, the MC would likewise not move, although the STD would increase showing outward dispersion.

DISCUSSION

Detecting and measuring invasion spatial patterns is a first step in achieving greater understanding of the dispersal patterns. We were able to measure the essential characteristics of

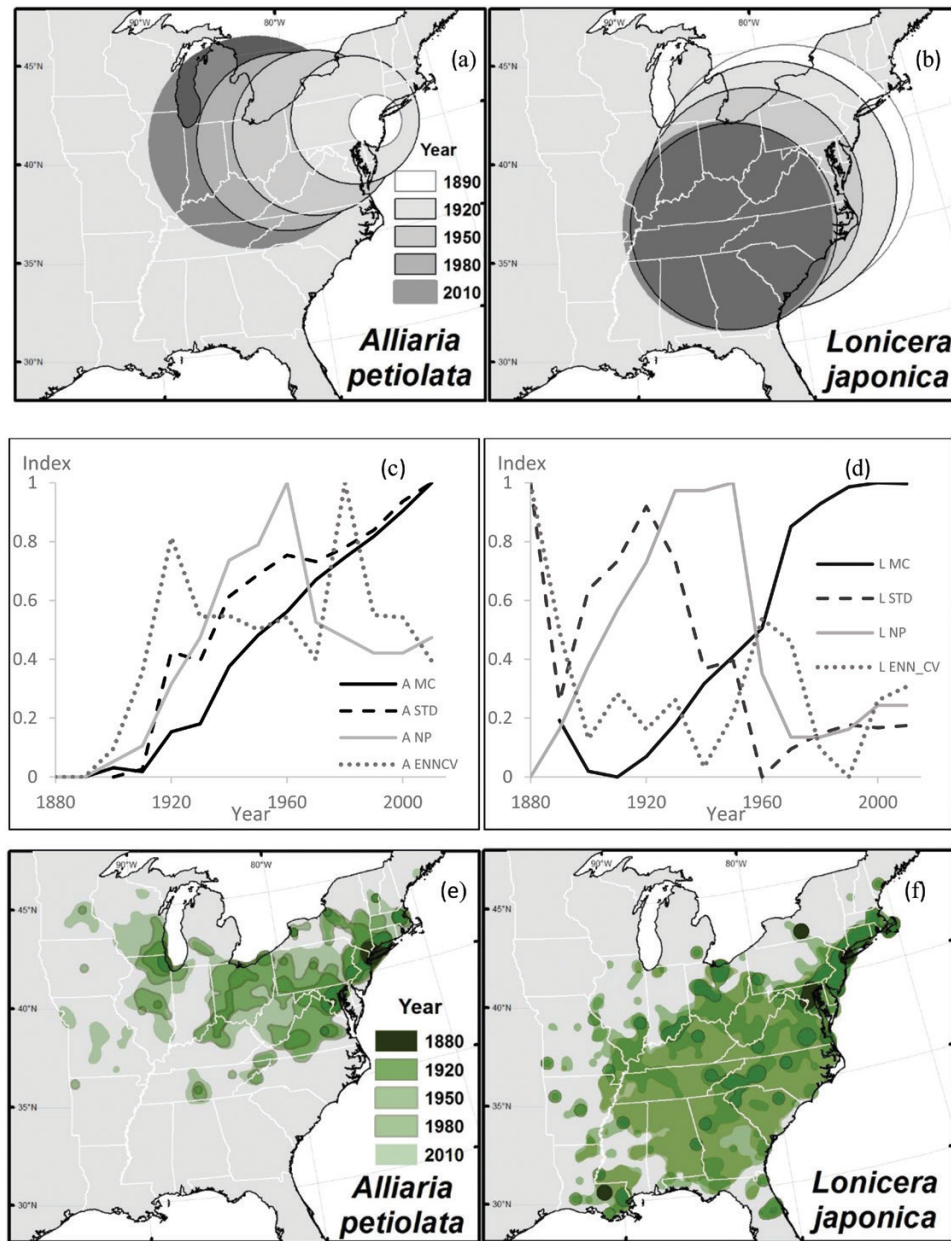


Figure 3: differing spatial patterns between *Alliaria petiolata* and *Lonicera japonica*, as revealed by four different metrics. Shown are mapped temporal changes in standard distances (STD) and mean centers seen by circle diameter and movement for (a) *A. petiolata* and (b) *L. japonica*; temporal changes in all four spatial metrics (STD, MC, NP and ENN_CV) for (c) *A. petiolata* and (d) *L. japonica*; and mapped temporal changes in the kernel density patches used to calculate NP and ENN_CV for (e) *A. petiolata* and (f) *L. japonica*. Note in (a) and (b) circles are stacked in different orders for visualization. For graphing ease, all metrics were normalized on a 0–1 scale with their own values. Maps use Albers equal area projection.

large-scale patterns of invasive species distributions, including diffusion, jump dispersal and changes in rates of spread (Fig. 1) by using a group of five differing techniques and metrics (SLR, STD, ENN_CV, NP and MC). When used in consort, these techniques and metrics proved capable of detecting both subtle and conspicuous differences between the spatiotemporal patterns of the two representative invasive plant species. Moreover, they provide a foundation for identification and study of the numerous other possible invasion scenarios.

Together, distance-based (STD and MC) and density-based (NP and ENN_CV) indices enabled us to quantify complex macroscale patterns, while the additional use of a SLR allowed the division of species invasion histories into distinct invasion phases. While many different methods have been employed through the year to quantify the rate of species invasions (Mihulka and Pyšek 2001; Aikio et al. 2010b; Liebhold et al. 2013), the ability of the SLR to sectionalize the expansion into discrete time periods had more utility to our study than the

smoother fit provided by a curve. This division was necessary to ensure that cross-species comparisons occurred during the same invasion phase.

We found many generally valuable metrics developed for landscape-level studies not suitable in our study due to their inapplicability at macroscales. We believe one of the main reasons for this inapplicability is that many of the highly employed landscape-level metrics are designed to differentiate between patch types at the raster cell level and our data do not have the spatial resolution necessary to give conclusive results of patch shape or aggregation. In addition, some of the landscape-level metrics are less intuitive to assess the observed macroscale attributes.

Although simple compared to other macroscale toolsets (Rangel *et al.* 2006), we feel this attribute underwrites the utility of our proposed metrics. More recent techniques employing α -hulls can additionally be employed with new geocoded data (Hui *et al.* 2014), while techniques such as the KDE we used allow for density estimation with less accurately located specimens. Given the resolution of much of the currently available data both simple and broad measures are often necessary in early exploratory analysis in many disciplines, and macroscale studies are likely no exception. While sets of metrics like these used to analyze spatial patterns provide an introductory step in gaining a deeper understanding of the underlying ecology of large-scale spatial patterns (Wu *et al.* 2011), they also may provide a straightforward, standardized method. Having a standardized method for investigating overall patterns can aid cross study comparison and further expose broad generalities (Cadotte *et al.* 2006). This recognition of large-scale spatial patterns can in turn guide further investigations into the causation of these patterns and a possibly provide greater understanding of interrelated and underlying processes affecting species invasions.

Specifically, it may prove useful to apply these metrics to evaluate the effects of life-history and functional traits on patterns of invasion. Some traits that aid species in establishment in novel environments may later hinder their expansion in later phases of invasion (van Kleunen *et al.* 2015). Therefore, the evaluation of the effects of species traits on spatiotemporal patterns needs to be invasion-phase specific. Additionally, cross-species comparisons made during the same invasion phase may provide increased understanding of life-history dynamics and may be of greater practical utility for prioritization of management actions (Williamson *et al.* 2005; van Kleunen *et al.* 2010). Our investigation showed that *L. japonica* reached a far higher maximum rate of spread during its expansion phase than did *A. petiolata*, which is echoed by the larger vacillations in *L. japonica*'s other metrics. Although *A. petiolata* has spread slower during its expansion phase, it currently does not show any reduction in that rate as the range continues to expand to the west and south. The species' proliferate seeds production and shade tolerance along with allopathic ability and lack of natural enemies are all factors that are likely fueling its invasion potential. Conversely,

during *L. japonica*'s expansion phase, the number of discrete patches (NP) plummeted to the same level seen in the late 1800's resultant from almost all of its expansion stemming from range infilling. Since that time, this species has become ubiquitous in southern forests and is the most widespread invasive plant species in the southeastern USA (Oswalt and Oswalt 2011). The species, even though considered noxious in several states, is still widely available in the horticultural markets (Lemke *et al.* 2011). This continued cultivation of an invasive species is likely contributing to the current slight rise in NP values (Fig. 3d) that may be due to the emergence of new, western patches (Fig. 3f) signaling that the previous expectations of range growth (Schierenbeck 2004) are just beginning to be realized.

Although we used these metrics with long-term herbarium data, they may also be useful for differentiating patterns among more recent invasions. To continue to have the ability to utilize these collections for research, there needs to be not only continued funding for preservation and digitation but also ongoing collection additions to document the changes to the flora due to ongoing global challenges such as climate change.

While this set of metrics can certainly aid in the investigation of biological invasions, part of their value rests in their ability to be applied to a wide range of investigations pertaining to spatial patterns. Possibilities may include changes in vegetation cover obtained from time series of aerial imagery, monitoring of wildlife migratory ranges or even evaluating trends within interdisciplinary research collaborations (Roush *et al.* 2007; Hoekman *et al.* 2010; Martin *et al.* 2015).

It should be noted that although we obtained a rate of spread from the SLR, our intent was not to estimate the exact rate. Herbarium specimens while very useful, tend to not report a species until possibly years after establishment. For this reason, we grouped both introductory slope segments into one phase of the plants invasion. Herbarium specimens could also be inherently biased due the sampling efforts, therefore our inclusion of multiple herbaria across the study area and the use of county centroid as sampling location could alleviate these spatial biases. Additionally, this metric set was specifically utilized with data that were confined to the eastern continental USA. If attempting to study a species expansion from far spread multiple sites or those that are divided by a waterbody or other barrier, estimates of spatial patterns calculated as we did here would likely be biased due to separate populations growing independently each affected by different factors and drivers.

For continued research into macrosystem patterns and processes, ecologists need to be able to quantify the patterns that emerge from the spatial heterogeneity in ecological processes that occur across large geographic areas (Heffernan *et al.* 2014). The utility of these techniques and metrics presented here for meeting this need lies within their minimal data requirements and their straightforward calculation and interpretation. Tools, such as these, can enhance our ability to detect and quantify spatial patterns, which is an important

step toward further understanding the causes and consequences of these patterns.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Plant Ecology* online.

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Conflict of interest statement. None declared.

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