

1 Title: Metrics for macroscale invasion and dispersal patterns

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13 Running Title: Macroscale invasion pattern metrics

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15

16 **ABSTRACT**

17

18 **Aim** The ability to quantitatively measure the continuum of macroscale patterns of
19 species invasion is a first step toward deeper understanding of their causal factors.

20 We took advantage of two centuries worth of herbarium data, to evaluate a set of
21 metrics to measure macroscale patterns, allowing cross-species comparisons of
22 invasive expansion across large geographic areas.

23

24 **Methods** We used herbarium specimens to reconstruct county-level invasion
25 histories for two non-native plants, (*Alliaria petiolata*, and *Lonicera japonica*), with
26 distinct spatiotemporal distribution patterns over the past two centuries. Metrics
27 from multiple disciplines, historically used at smaller spatial scales, were then
28 evaluated for their ability to detect macroscale spatial diffusion and amount of
29 directional expansion. Metrics were further assessed for their ease of use, data
30 requirements, independence from other metrics, and intuitiveness of interpretation.

31

32 **Important Findings** We identified four suitable metrics for distinguishing differences
33 in spatial patterns: (1) standard distance, (2) number of patches (3) Euclidean nearest
34 neighbor summary class statistic coefficient of variation, and (4) mean center that
35 when applied to county-level presence data allowed us to determine the directions by
36 which distributions expanded, and if distributions increased via outward expansion,
37 infilling, and/or jump dispersal events. These metrics when compared during the
38 same invasion phase are capable of quantifying macroscale variability among species
39 in their distributional and dispersal patterns. Being able to quantify differences

40 among species in these patterns is important in understanding the drivers of species
41 dispersal patterns. These metrics therefore represent a simple yet thorough toolset
42 for achieving this goal.

43

44 **Keywords**

45 *Alliaria petiolata*, diffusion, herbarium, jump dispersal, *Lonicera japonica*, plant
46 invasions

47

48 **Introduction**

49

50 Patterns of ecological processes across large geographic areas emerge from complex,
51 cross-scale interactions among many biotic and abiotic factors. This complexity
52 inevitably contributes to macroscale patterns of species distribution and dispersal.
53 Understanding the factors that contribute to these patterns has long interested
54 various sub-disciplines of ecology such as paleoecology and biogeography
55 (Dobzhansky 1950, Matthew 1914, Pianka 1966), and more recently macrosystem
56 ecology (Fei *et al.* 2016), and is becoming more crucial for understanding macroscale
57 patterns of a leading component of global change—biological invasions (Iannone *et al.*
58 2015, Mooney *et al.* 2001, Ricciardi 2007, Strayer *et al.* 2006). As a beginning step of
59 understanding what drives macroscale dispersal patterns, one must first be able to
60 effectively quantify various characteristics of species expansion patterns both over
61 time and across large geographic areas.

62 Species distributions change via a series of diffusion and jump dispersal events
63 (Shigesada *et al.* 1997, Wilkinson 2001), leading to the continued evolution of spatial

64 patterns over time (See Fig.1 for examples). Being able to quantify the variability in
65 these changing spatial patterns, along with the directional movement and rates of
66 spread, can help to reveal differences and similarities in patterns at different invasion
67 stages of a given species and among different species. The quantification of these
68 patterns, when paired with further consideration of species traits and environmental
69 conditions, can provide increased understanding into the factors contributing to
70 species expansion (Rouget *et al.* 2003). Despite the many indices developed to
71 quantify spatial patterns, there is likely no single metric able to completely
72 encapsulate the complexities of large-scale dispersal patterns (Pysek *et al.* 2005). The
73 quantification of spatiotemporal changes in species distributions across large
74 geographic areas will likely require multiple metrics. Identifying these metrics,
75 however, is challenging due to the lack of long-term spatiotemporal data pertaining to
76 species distributions.

77 The main objective of this investigation is to identify a set of metrics applicable
78 to macroscale pattern recognition of invasive plant species expansions using
79 methodologies already tested at smaller scales. The utility of these indices will be
80 evaluated using collected herbarium specimen supplied spatiotemporal data for two
81 invasive plant species, *Alliaria petiolata* (M. Bieb) Cavara & Grande (garlic mustard)
82 and *Lonicera japonica* Thunb. (Japanese honeysuckle), that exhibit distinctly different
83 macroscale patterns of spread. Historically, herbarium specimens have provided
84 researchers with a wealth of knowledge concerning the taxonomy, systematics, and
85 evolution of collected plant material. Recently, the usage of these collections has
86 been amplified into genetics, spatial ecology, and climate change. In this study, we

87 also want to highlight the use of herbarium collections in understanding macroscale
88 invasion patterns and processes, both spatially and temporally.

89 The outcomes of this investigation will provide a set of metrics that can be
90 used at macroscales to quantify spatiotemporal patterns of plant species dispersal,
91 which can aid better understanding of those patterns, and perhaps of other ecological
92 processes. These findings will also provide a greater understanding of macroscale
93 patterns of spread for invasive species, which is of practical utility given the
94 contribution of these species to overall global change (Fei *et al.* 2014, Simberloff 2011,
95 Vitousek *et al.* 1997).

96

97 **MATERIALS AND METHODS**

98

99 **Data selection and acquisition**

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101 To estimate patterns of spread for both species, we determined the timing of county-
102 level presence of each invader for the eastern United States of America (USA) by using
103 herbarium records we compiled covering the past two centuries. Each species
104 exhibited variable rates of spread over the courses of their invasion histories, allowing
105 us to identify different phases of their invasions (see Fig. 1e for definition of invasion
106 phase). Specimens for *A. petiolata* and *L. japonica* were collected from approximately
107 120 differing herbaria and other published sources (see Table S1 in Appendix S1).
108 Following protocols by (Delisle *et al.* 2003), specimens lacking locations, dates, or
109 which were obviously cultivated were discarded and the species was considered to
110 persist in a county once it was collected there. Historically, herbarium specimen

111 records have been shown to be a viable proxy for species range and expansion data
112 (Aikio *et al.* 2010a, Pysek *et al.* 1995), and have also been used successfully to
113 reconstruct the timing and extent of invasion (Barney 2006, Fuentes *et al.* 2008,
114 Kannan *et al.* 2013). While herbarium data are known to exhibit both spatial and
115 temporal bias due to non-random sampling efforts (Loiselle *et al.* 2008), the purpose
116 of our study was to described and differentiate spatial patterns and not to calculate
117 specific spread rates of the actual species invasions, affording us the ability to assume
118 these biases to cause minimal effects on the results.

119 Each of the species has a long invasion history in the USA, being introduced in
120 the early 19th century (Munger 2001, Schierenbeck 2004). *Alliaria petiolata*, an
121 upright obligate biennial forb, is believed to have been introduced for use as a garden
122 herb and medicinal purposes (Munger 2001). Due to its prolific seed production
123 (Nuzzo 1999), and its primary mechanism of dispersal by epizoochory (Cavers *et al.*
124 1979), its recent spread is believed to be mostly accidental (US Forest Service 2005).
125 In contrast, *L. japonica*, a perennial flowering vine, was introduced in multiple
126 locations through the horticultural trade because of its fragrance and ease of growth
127 (Lemke *et al.* 2011). The variability between these species in their growth forms,
128 modes of introduction, and life history traits likely influences their invasion
129 trajectories and current range sizes (Moravcová *et al.* 2015).

130

131 **Metrics**

132

133 Spatiotemporal dynamics of a species' range expansion encompasses a vast
134 continuum of spatial patterns that lie within the general bounds of diffusion (i.e.,

135 gradual and regular spread, radiating in concentric circles) and jump dispersal (i.e.,
136 long distance spread to locations outside of a species current range) (Pielou 1979,
137 Simberloff *et al.* 1997). To capture the entire gamut of potential spatial patterns in
138 range expansion and infilling, it is essential to have metrics that measure both the
139 density of, and the distances among, species observations. In addition, to determine if
140 spatial patterns of expansion vary among invasion phases, we need a quantitative
141 method for detecting abrupt changes in rates of spread, which likely signify points in
142 time where these phases begin and end. This distinction among invasion phases can
143 also help to ensure that comparisons among species in spatial patterns occur during
144 the same invasion phases, making these comparisons more meaningful. Furthermore,
145 to ensure the greatest utility and applicability of these metrics, we chose metrics
146 (Table 1) assessing for ease of use, data requirements, independence from the other
147 metrics, intuitiveness, and their ability to distinguish spatiotemporal patterns at the
148 macroscale.

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

$$157 \quad X' = \frac{X - X_{min}}{X_{max} - X_{min}} \quad (1)$$

158

159 To estimate the degree to which distributions were dispersed throughout a
160 species' range and the directional migration of each species, we utilized two distance-
161 based spatial statistic metrics: *standard distance* (STD) and *mean center* (MC). We
162 calculated these metrics from the latitude and longitude (x,y coordinates) of the
163 centroid locations of the counties from which herbarium specimens were collected.
164 The STD metric estimates the radius of the circle that encompasses one standard
165 deviation of our sample points, i.e. centroids of the invaded counties. MC of the
166 distribution is calculated from the average of the (x, y) geographical coordinates of all
167 the input points (in our case county centroids) at each time period (See Table 1). We
168 measured the Euclidean distance between the original geographical center of the
169 distribution, i.e., the centroid from which the invasion started, and succeeding decadal
170 calculations of the MC coordinates to track the overall shifting "weight" of the species
171 distribution through time.

172 By using kernel density estimation (KDE) on the county centroids we produced
173 a smoothed raster surface reflecting the areas of higher density of collected
174 specimens. Erring on the conservative side, we performed calculations only on the 75
175 percent volume curves (PVC) (Geospatial Modeling Environment, Version 0.7.3.0)
176 based on prior recommendations (Borger *et al.* 2006). This procedure enabled us to
177 identify and then quantify true expanding colonies versus an outlying single collection.
178 Using the KDE patches, two density-based metrics were calculated: *coefficient of*
179 *variation of the Euclidean nearest neighbor* (ENN_CV) and the *number of patches* (NP).
180 These metrics were then used respectively, to identify jump dispersal events and to
181 estimate intra-range species dispersion. The coefficient of variation is a ratio of
182 dispersion that shows the extent of variability of the sample in relation to its mean (in

183 our case, the measured Euclidean distances between the KDE patches at that time),
184 and is calculated by taking the standard deviation of a frequency distribution and
185 dividing it by the mean of that same distribution (i.e., s/\bar{x}). The metric *number of*
186 *patches* (NP) is a simple count of the count of discrete KDE patches that are formed at
187 the 75 PVC during each time period.

188 We also explored the utility of numerous other metrics (see Table S2 in
189 Appendix S2), but for multiple reasons found them to be less applicable to
190 macroscales. We chose segmented regression over others' techniques (Aikio *et al.*
191 2010b, Gilbert *et al.* 2010, Larkin 2012, Liebhold *et al.* 1992, Liebhold *et al.* 2013,
192 Mihulka *et al.* 2001, Tobin *et al.* 2007) because of its ability to detect changes in rates
193 of spread, and thus transitions between different invasion phases (e.g. Fig. 1e). We
194 also measured point distances between the centroids of all invaded counties and
195 evaluated the effectiveness of using the maximum, mean, and standard deviation of
196 those distances as metrics of spatial dispersion. These metrics were not chosen,
197 because relative to STD, they did not provide a significant improvement in pattern
198 description and they required more data and computational time. Additionally, we
199 investigated other metrics aimed at quantifying aspects of area and edge, shape
200 complexity, and aggregation. We opted not to utilize these landscape-level metrics
201 because either they were incapable of detecting spatial variability in our
202 presence/absence data at the much larger spatial extent of our investigation, or they
203 were less intuitive.

204 Spatial metrics were calculated for decadal time intervals. Segmented
205 regressions were conducted using the Segmented package in R (Muggeo 2008, R Core
206 Team 2015). Kernel density estimation and all distance geographic metrics were

207 calculated using the Albers equal area conic projection (USGS) and ARCGIS 10.2.2 (Esri,
208 Redlands, CA, USA). Landscape metrics were calculated utilizing FRAGSTATS (v4.2.1.603)
209 (McGarigal *et al.* 2012). The final set of five metrics were verified for independence
210 (see Figure S3 in Appendix S3) and the four spatial metrics were normalized from 0–1
211 to facilitate cross-species comparisons (see equation 1 above).

212

213 **RESULTS**

214

215 **Thresholds and Rates of Spread**

216

217 Assisted by segmented linear regression, we found three changes in rates of spread
218 corresponding to two invasion phases for *A. petiolata* (Fig. 2a) and four changes in
219 rates of spread corresponding to three possible invasion phases for *L. japonica* (Fig.
220 2b). The first two line segments for the invasion curves of both species likely signify
221 establishment phases. This distinction is due to both the relatively lower slope values
222 for these line segments and the paucity of herbarium specimens collected during
223 these periods. The subsequent segments, where rates of expansion increase, likely
224 signify expansion phases. *Alliaria petiolata* showed a tripling in its rate of spread after
225 1960, which it still maintains. Comparably, the non-scaled counts show *L. japonica*
226 accumulated 25 counties per year during its expansion phase versus *A. petiolata*'s nine
227 counties per year, but *L. japonica* only maintained that rate of spread for
228 approximately 20 years. After that period *L. japonica*'s rate of spread declined,
229 suggesting it is approaching a saturation phase. Segmented linear regression revealed
230 comparable values in the rate of spread for both species during their establishment

231 phase, and the species' shift to expansion phase occurred in close time proximity to
232 each other. Yet, the differences in normalized rates of spread during expansion phase
233 (0.015 normalized units for *A. petiolata* and 0.025 normalized units for *L. japonica*)
234 allowed us to investigate whether varying rates of spread would affect the utility of
235 our spatial metrics.

236

237 **Diffusion and Jump dispersal**

238

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

252 We found both species experienced initial increases, followed by decreases, in
253 the degree of spatial dispersion exhibited by their distribution. This pattern is
254 revealed by the initial increase and then later merging of the kernel density patches

255 (NP) (Fig. 3 e & f). The NP metric allows investigation of the species' tendency to
256 enlarge its territory either by more dispersed colonies or by the expanding colonies
257 growing together into clumps. This knowledge used with the results from STD, is able
258 to distinguish overall long term changes in dispersion. Both *A. petiolata* and *L.*
259 *japonica* show an increase in NP from their initial colonization until the maximum NP
260 count occurs during the transition from the establishment to expansion phase (Fig. 3c
261 & d). Throughout their expansion phase, the NP values for both species continually
262 decrease, showing patch coalescence into larger, less numerous colonies. *Lonicera*
263 *japonica's* NP values plummet, while those of *A. petiolata* continue to maintain
264 moderate values. The plummeting NP values of *L. japonica* are largely due to
265 increased density from infilling of the species' range (Fig. 3f). The moderate yet stable
266 NP values of *A. petiolata* are due to the balancing of new patches occurring over time
267 as this species' range expands westward, while older patches simultaneously merge
268 together (Fig. 3e).

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

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

284

285 **Directional Expansion**

286 Movement through time of the mean center (MC) location of the distribution of each
287 species revealed the directional trajectory of its expansion. The graph of the MC
288 distances from first collection point of *A. petiolata* shows a continual linear increase
289 indicating persistent expansive movement away from its initial location, while that of
290 *L. japonica* shows a rapid decline in directional movement after 1960 (Figs. 3a, b, c,
291 &d). While the continual migration of the MC away from a species' introduction point
292 indicates directional movement, a stationary MC requires further investigation.

293 Stationary MC values can either be indicative of a range infilling, as seen in *L.*
294 *japonica*'s later years (Fig. 3e and typified in Fig. 1d), or stem from equal expansion in
295 all directions radiating outward from a species' initial introduction point. During *L.*
296 *japonica*'s recent history, and most current invasion phase, all four spatial metrics
297 (STD, MC, NP and ENN_CV) level off, while the rate of spread decreased (Fig. 2b),
298 suggesting the distribution of this species to be stabilizing. Alternately, if a species is
299 expanding equally in all directions, the MC would likewise not move, although the STD
300 would increase showing outward dispersion.

301

302 **DISCUSSION**

303

304 Detecting and measuring invasion spatial patterns is a first step in achieving greater
305 understanding of the dispersal patterns. We were able to measure the essential
306 characteristics of large-scale patterns of invasive species distributions, including
307 diffusion, jump dispersal, and changes in rates of spread (Fig.1) by using a group of
308 five differing techniques and metrics (SLR, STD, ENN_CV, NP, and MC). When used in
309 consort, these techniques and metrics proved capable of detecting both subtle and
310 conspicuous differences between the spatiotemporal patterns of the two invasive
311 plant species. Together, distance based (STD & MC), and density based (NP, ENN_CV)
312 indices enabled us to quantify complex macroscale patterns, while the additional use
313 of a segmented linear regression (SLR) allowed the division of species invasion
314 histories into distinct invasion phases. This division was necessary to ensure that
315 cross-species comparisons occurred during the same invasion phase.

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

323 Although simple compared to other macroscale toolsets (Rangel *et al.* 2006),
324 we feel this attribute underwrites the utility of our proposed metrics. Both simple and
325 broad measures are often necessary in early exploratory analysis in many disciplines,
326 and macroscale studies are likely no exception. While sets of metrics like these used

327 to analyze spatial patterns provide an introductory step in gaining a deeper
328 understanding of the underlying ecology of large-scale spatial patterns (Wu *et al.*
329 2011), they also may provide a straightforward, standardized method. Having a
330 standardized method for investigating overall patterns can aid cross study comparison
331 and further expose broad generalities (Cadotte *et al.* 2006). This recognition of large-
332 scale spatial patterns can in turn guide further investigations into the causation of
333 these patterns and a possibly provide greater understanding of interrelated and
334 underlying processes affecting species invasions.

335 Specifically, it may prove useful to apply these metrics to evaluate the effects
336 of life history and functional traits on patterns of invasion. Some traits that aid
337 species in establishment in novel environments may later hinder their expansion in
338 later phases of invasion (van Kleunen *et al.* 2015). Therefore, the evaluation of the
339 effects of species traits on spatiotemporal patterns needs to be invasion-phase
340 specific. Additionally, cross-species comparisons made during the same invasion
341 phase may provide increased understanding of life history dynamics and may be of
342 greater practical utility for prioritization of management actions (van Kleunen *et al.*
343 2010, Williamson *et al.* 2005). Our investigation showed that *L. japonica* reached a far
344 higher maximum rate of spread during its expansion phase than did *A. petiolata*,
345 which is echoed by the larger vacillations in *L. japonica*'s other metrics. During *L.*
346 *japonica*'s expansion phase the number of discrete patches (NP) plummeted to the
347 same level seen in the late 1800's resultant from almost all of its expansion stemming
348 from range infilling. Since that time this species has become ubiquitous in southern
349 forests and is the most widespread invasive plant species in the southeastern USA
350 (Oswalt *et al.* 2011). The current slight rise in NP values (Fig. 3d) may be due to the

351 emergence of new, western patches (Fig. 3f) signaling that the previous expectations
352 of range growth (Schierenbeck 2004) are just beginning to be realized.

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

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

365 It should be noted that although we obtained a rate of spread from the SLR,
366 our intent was not to estimate the exact rate. Herbarium specimens while very useful,
367 tend to not report a species until possibly years after establishment. For this reason
368 we grouped both introductory slope segments into one phase of the plants invasion.
369 Additionally, this metric set was specifically utilized with data that were confined to
370 the eastern continental US. If attempting to study a species expansion from far spread
371 multiple sites or those that are divided by a waterbody or other barrier, estimates of
372 spatial patterns calculated as we did here would likely be biased due to separate
373 populations growing independently.

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

382

383

384 **Supporting Information**

385 Additional Supporting Information may be found in the online version of this article.

386

387 **Appendix S1** List of herbaria from which specimens were obtained.

388 **Appendix S2** Full list of metrics investigated.

389 **Appendix S3** Associations among final metrics.

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REFERENCES

- 402
403
- 404 Aikio S, Duncan RP, Hulme PE (2010a) Herbarium records identify the role of long-distance
405 spread in the spatial distribution of alien plants in New Zealand. *Journal of Biogeography*
406 **37**:1740-1751.
- 407 Aikio S, Duncan RP, Hulme PE (2010b) Lag-phases in alien plant invasions: separating the facts
408 from the artefacts. *Oikos* **119**:370-378.
- 409 Barney JN (2006) North American history of two invasive plant species: phytogeographic
410 distribution, dispersal vectors, and multiple introductions. *Biological Invasions* **8**:703-717.
- 411 Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006)
412 Effects of sampling regime on the mean and variance of home range size estimates. *Journal of*
413 *Animal Ecology* **75**:1393-1405.
- 414 Cadotte MW, Murray BR, Lovett-Doust J (2006) Ecological patterns and biological invasions:
415 Using regional species inventories in macroecology. *Biological Invasions* **8**:809-821.
- 416 Cavers PB, Heagy MI, Kokron RF (1979) Biology Of Canadian Weeds .35. *Alliaria-petiolata* (M
417 Bieb) Cavara And Grande. *Canadian Journal of Plant Science* **59**:217-229.
- 418 Delisle F, Lavoie C, Jean M, Lachance D (2003) Reconstructing the spread of invasive plants:
419 taking into account biases associated with herbarium specimens. *Journal of Biogeography*
420 **30**:1033-1042.
- 421 Dobzhansky T (1950) Evolution in the tropics. *American Scientist* **38**:209-221.
- 422 Environmental Systems Research Institute (2014) ArcGIS (GIS software), Version 10.2.2.,
423 Redlands, CA.
- 424 Fei S, Phillips J, Shouse M (2014) Biogeomorphic Impacts of Invasive Species. In Futuyama DJ
425 (ed) *Annual Review of Ecology, Evolution, and Systematics, Vol 45*, Vol. 45, 69-+.
- 426 Fei SL, Guo QF, Potter K (2016) Macrosystems ecology: novel methods and new
427 understanding of multi-scale patterns and processes. *Landscape Ecology* **31**:1-6.
- 428 Fuentes N, Ugarte E, Kuehn I, Klotz S (2008) Alien plants in Chile: inferring invasion periods
429 from herbarium records. *Biological Invasions* **10**:649-657.
- 430 Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading
431 populations. *Ecography* **33**:809-817.

- 432 Heffernan JB, Soranno PA, Angilletta MJ, Buckley LB, Gruner DS, Keitt TH, Kellner JR,
433 Kominoski JS, Rocha AV, Xiao JF, Harms TK, Goring SJ, Koenig LE, McDowell WH, Powell H,
434 Richardson AD, Stow CA, Vargas R, Weathers KC (2014) Macrosystems ecology:
435 understanding ecological patterns and processes at continental scales. *Frontiers in Ecology*
436 *and the Environment* **12**:5-14.
- 437 Hoekman J, Frenken K, Tijssen RJW (2010) Research collaboration at a distance: Changing
438 spatial patterns of scientific collaboration within Europe. *Research Policy* **39**:662-673.
- 439 Iannone BV, Oswalt CM, Liebhold AM, Guo QF, Potter KM, Nunez-Mir GC, Oswalt SN,
440 Pijanowski BC, Fei SL (2015) Region-specific patterns and drivers of macroscale forest plant
441 invasions. *Diversity and Distributions* **21**:1181-1192.
- 442 Kannan R, Shackleton CM, Shaanker RU (2013) Reconstructing the history of introduction and
443 spread of the invasive species, Lantana, at three spatial scales in India. *Biological Invasions*
444 **15**:1287-1302.
- 445 Larkin DJ (2012) Lengths and correlates of lag phases in upper-Midwest plant invasions.
446 *Biological Invasions* **14**:827-838.
- 447 Lemke D, Hulme PE, Brown JA, Tadesse W (2011) Distribution modelling of Japanese
448 honeysuckle (*Lonicera japonica*) invasion in the Cumberland Plateau and Mountain Region,
449 USA. *Forest Ecology and Management* **262**:139-149.
- 450 Liebhold AM, Halverson JA, Elmes GA (1992) Gypsy Moth Invasion in North America: A
451 Quantitative Analysis. *Journal of Biogeography* **19**:513-520.
- 452 Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A
453 highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and*
454 *Distributions* **19**:1208-1216.
- 455 Loiselle BA, Jorgensen PM, Consiglio T, Jimenez I, Blake JG, Lohmann LG, Montiel OM (2008)
456 Predicting species distributions from herbarium collections: does climate bias in collection
457 sampling influence model outcomes? *Journal of Biogeography* **35**:105-116.
- 458 Martin SL, Jasinski BL, Kendall AD, Dahl TA, Hyndman DW (2015) Quantifying beaver dam
459 dynamics and sediment retention using aerial imagery, habitat characteristics, and economic
460 drivers. *Landscape Ecology* **30**:1129-1144.
- 461 Matthew WD (1914) Climate And Evolution. *Annals of the New York Academy of Sciences*
462 **24**:171-318.

- 463 McGarigal K, Cushman SA, Neel MC, Ene E (2012) FRAGSTATS: Spatial Pattern Analysis
464 Program for Categorical and Continuous Maps (v4.2.1.603): Computer software program
465 produced by the authors at the University of Massachusetts, Amherst.
- 466 Mihulka S, Pyšek P (2001) Invasion history of *Oenothera* congeners in Europe: a comparative
467 study of spreading rates in the last 200 years. *Journal of Biogeography* **28**:597-609.
- 468 Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. *Proceedings of the*
469 *National Academy of Sciences of the United States of America* **98**:5446-5451.
- 470 Moravcová L, Pyšek P, Jarošík V, Pergl J (2015) Getting the Right Traits: Reproductive and
471 Dispersal Characteristics Predict the Invasiveness of Herbaceous Plant Species. *PLoS One*
472 **10**:e0123634.
- 473 Muggeo VMR (2008) segmented: an R Package to Fit Regression Models with Broken-Line
474 Relationships. *R News*.
- 475 Munger GT (2001) *Alliaria petiolata* *Landscape Ecology*, Rocky Mountain Research Station,;
476 Fire Sciences Laboratory (Producer).
- 477 Nuzzo V (1999) Invasion pattern of herb garlic mustard (*Alliaria petiolata*) in high quality
478 forests. *Biological Invasions* **1**:169-179.
- 479 Oswalt SN, Oswalt CM (2011) The extent of selected nonnative invasive plants on southern
480 forest lands. In Fei S, Lhotka JM, Stringer JW, Gottschalk KW, Miller GW (eds) *17th central*
481 *hardwood forest conference*, Lexington, KY: U.S. Department of Agriculture, Forest Service,
482 Northern Research Station, 447-459.
- 483 Pianka ER (1966) Latitudinal Gradients In Species Diversity - A Review Of Concepts. *American*
484 *Naturalist* **100**:33-&.
- 485 Pielou EC (1979) *Biogeography*, New York: Wiley.
- 486 Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: Linking pattern to
487 process. *Ecoscience* **12**:302-315.
- 488 Pyšek P, Prach K (1993) Plant Invasions And The Role Of Riparian Habitats - A Comparison Of 4
489 Species Alien To Central-Europe. *Journal of Biogeography* **20**:413-420.
- 490 Pyšek P, Prach K (1995) Invasion dynamics of *Impatiens glandulifera* - A Century Of Spreading
491 Reconstructed. *Biological Conservation* **74**:41-48.

- 492 R Core Team (2015) R: A language and environment for statistical computing, Vienna, Austria:
493 R Foundation for Statistical Computing.
- 494 Rangel TFLVB, Felizola Diniz-Filho JA, Bini LM (2006) Towards an integrated computational
495 tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*
496 **15**:321-327.
- 497 Ricciardi A (2007) Are modern biological invasions an unprecedented form of global change?
498 *Conservation Biology* **21**:329-336.
- 499 Rouget M, Richardson David M (2003) Inferring Process from Pattern in Plant Invasions: A
500 Semimechanistic Model Incorporating Propagule Pressure and Environmental Factors. *The*
501 *American Naturalist* **162**:713-724.
- 502 Roush W, Munroe JS, Fagre DB (2007) Development of a spatial analysis metho using ground-
503 based repeat photography to detect changes in the alpine treeline ecotone, Glacier National
504 Park, Montana, USA. *Arctic Antarctic and Alpine Research* **39**:297-308.
- 505 Schierenbeck KA (2004) Japanese honeysuckle (*Lonicera japonica*) as an invasive species;
506 history, ecology, and context. *Critical Reviews in Plant Sciences* **23**:391-400.
- 507 Shigesada N, Kawasaki K (1997) Biological invasions: theory and practice, UK: Oxford
508 university press.
- 509 Simberloff D (2011) How common are invasion-induced ecosystem impacts? *Biological*
510 *Invasions* **13**:1255-1268.
- 511 Simberloff D, Schmitz DC, Brown TC (1997) Strangers in paradise: impact and management of
512 nonindigenous species in Florida, Washington, D.C.: Island press.
- 513 Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of
514 species invasions. *Trends in Ecology & Evolution* **21**:645-651.
- 515 Tobin PC, Liebhold AM, Roberts EA (2007) Comparison of methods for estimating the spread
516 of a non-indigenous species. *Journal of Biogeography* **34**:305-312.
- 517 US Forest Service (2005) Factsheets: Garlic Mustard (*Alliaria petiolata*). In Agriculture UDo (ed)
518 *Invasive Plants Fact Sheets*, St. Paul, MN, 7p.
- 519 van Kleunen M, Dawson W, Maurel N (2015) Characteristics of successful alien plants.
520 *Molecular Ecology* **24**:1954-1968.

- 521 van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010) Are invaders
522 different? A conceptual framework of comparative approaches for assessing determinants of
523 invasiveness. *Ecology Letters* **13**:947-958.
- 524 Vitousek PM, Dantonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species:
525 A significant component of human-caused global change. *New Zealand Journal of Ecology*
526 **21**:1-16.
- 527 Wilkinson DM (2001) *Dispersal: Biogeography eLS*: John Wiley & Sons, Ltd.
- 528 Williamson M, Pysek P, Jarosik V, Prach K (2005) On the rates and patterns of spread of alien
529 plants in the Czech Republic, Britain, and Ireland. *Ecoscience* **12**:424-433.
- 530 Wu J, Jenerette GD, Buyantuyev A, Redman CL (2011) Quantifying spatiotemporal patterns of
531 urbanization: The case of the two fastest growing metropolitan regions in the United States.
532 *Ecological Complexity* **8**:1-8.
- 533

534 **BIOSKETCH**

535 This research was performed while Teresa L. Clark was a USDA National Needs Fellow
536 in the Ecological Sciences and Engineering Interdisciplinary Graduate Program, and a
537 Master's student in the Department of Forestry and Natural Resources at Purdue
538 University. Her research focused on large-scale spatiotemporal expansion patterns of
539 nonnative plant species.

540

541 **Author contributions:** All authors contributed to the conceptualization and writing of
542 this paper.

543 TABLES

Table 1. Metrics used to quantify macroscale patterns of spread including their equations and specific use			
Metric	Abreviation	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.

545 **FIGURE LEGENDS**

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

552

553 **Figure 2.** Results of segmented linear regressions with scaled slopes \pm se values revealing (a)
554 an establishment and expansion phase for *A. petiolata* and (b) establishment and expansion
555 phase for *L. japonica*, with this species potentially approaching a saturation phase.

556

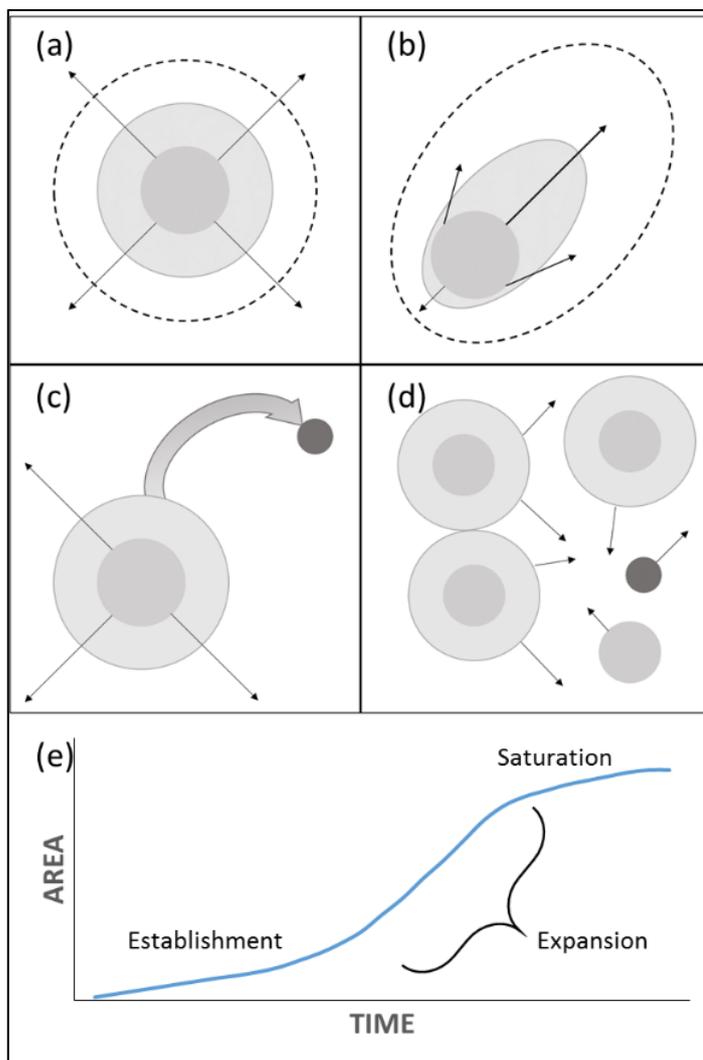
557 **Figure 3.** Differing spatial patterns between *A. petiolata* and *L. japonica*, as revealed by four
558 different metrics. Shown are: mapped temporal changes in standard distances (STD) and
559 mean centers seen by circle diameter and movement for (a) *A. petiolata* and (b) *L. japonica*;
560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

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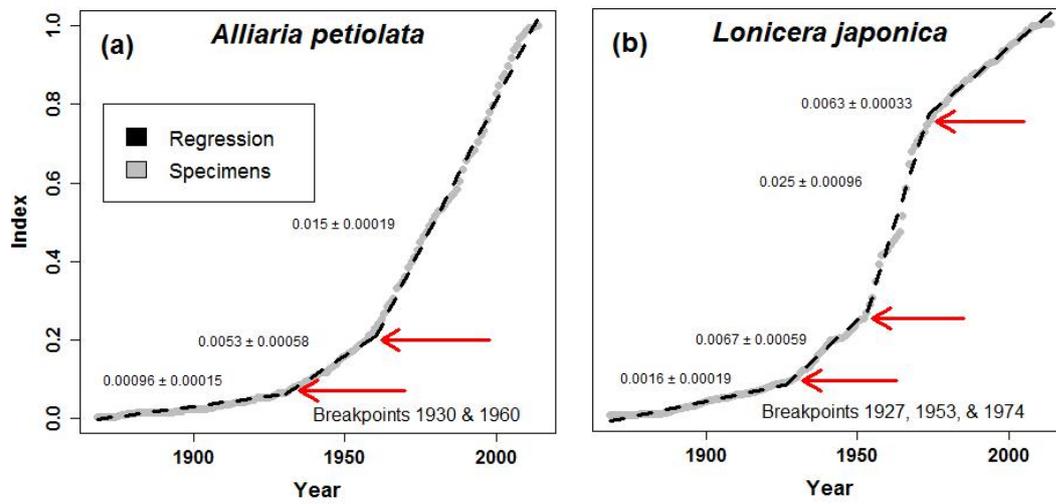
567 **FIGURES**

568

**Figure 1.**

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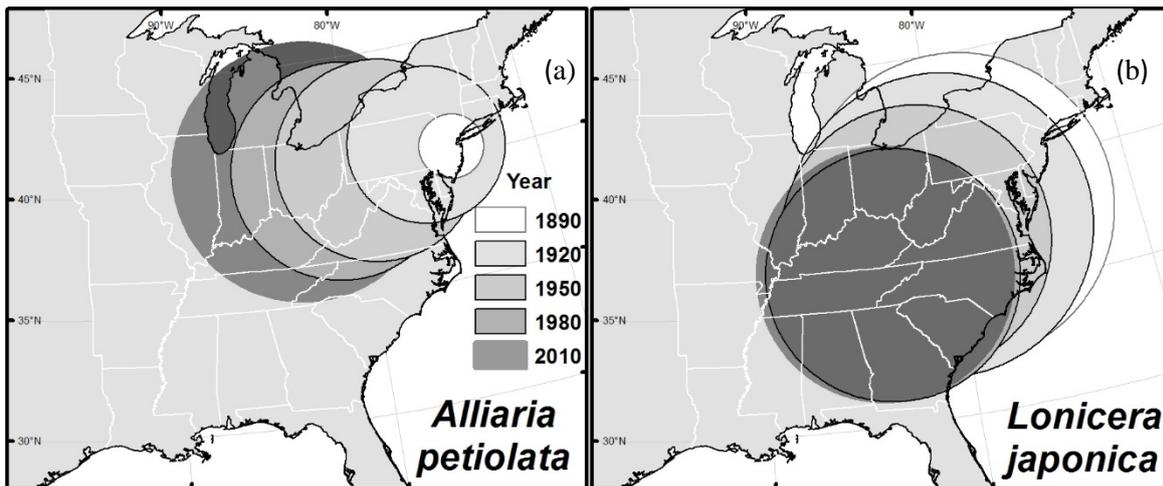


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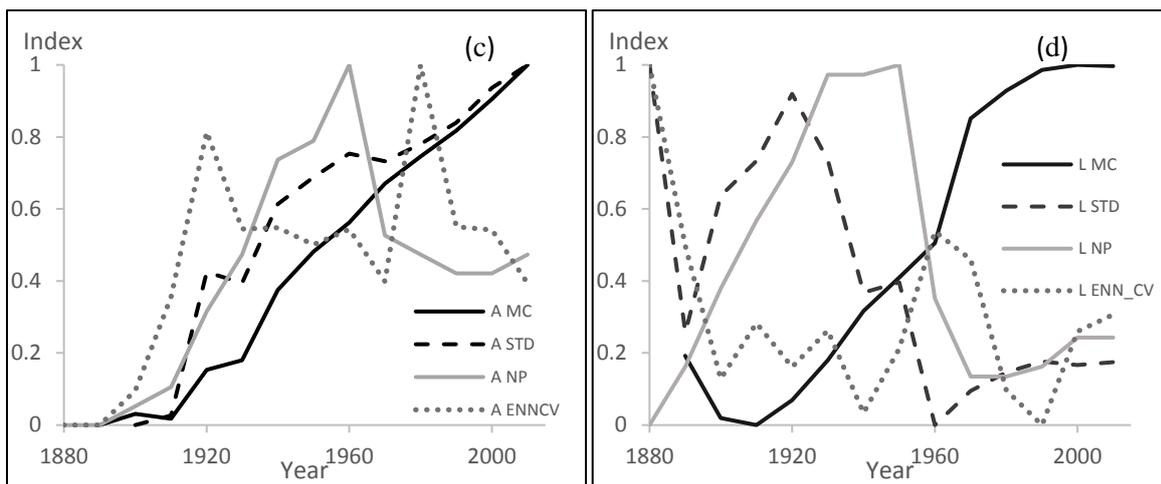
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573 **Figure 2.**

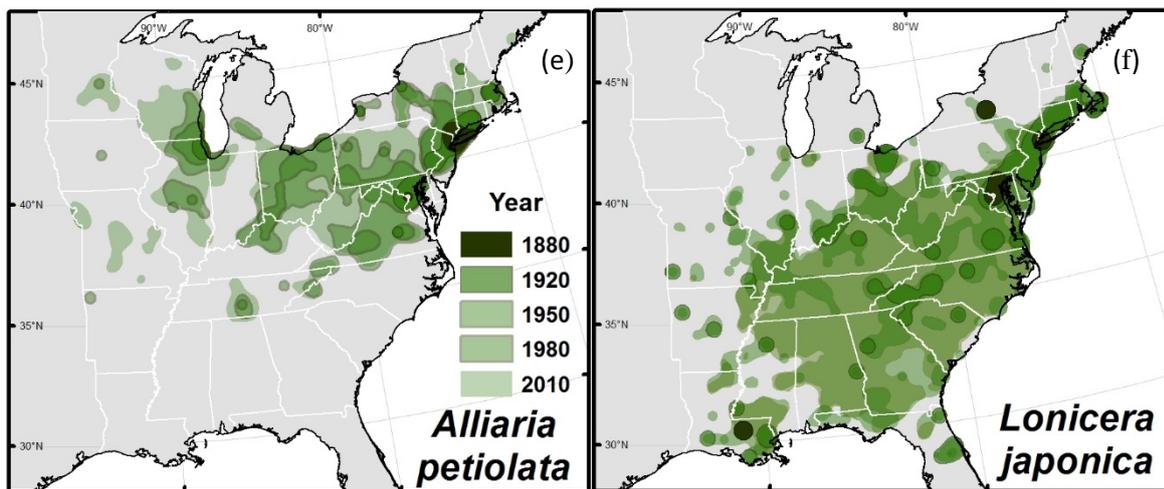
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579 **Figure 3.**

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